11 TRANSPORT IN PLANTS

Plants lack both interstitial fluid as well as a regular circulation system. Even then they have to move (transport) various types of substances (gases, minerals, water, hormones, photosynthates and organic solutes) not only to short distance (from one cell to another or from one tissue to another) but also to very **long distances** such as water from roots to tops of plants or photosynthates from leaves to tips of roots. Substances move over **short distances** through diffusion and active transport supplemented by cytoplasmic streaming. Long distance transport occurs through vascular systems, xylem and phloem. This transport of substances over longer distances through the vascular tissue, *i.e.,* xylem and phloem, is called **translocation**. It occurs through **mass flow**. The direction of translocation is essentially **unidirectional** in case of water (from root to stem, leaves, flowers and fruits). It is **multidirectional** in case of minerals and organic solutes. Organic compounds are synthesised in leaves. They are exported to all other parts including every living cell, growing points, fruits and storage organs. Storage organs re-export the organic nutrients when new growth is to take place. Certain parts re-export the products of their own biosynthetic activities. Mineral nutrients are primarily picked up by roots. They are passed out upwardly to leaves, stem and growing regions. Leaves re-export many of these minerals in organic form. Senescent organs and leaves pass out most of their nutrients, especially the mineral ones, before falling down from the plant. Plant hormones and other chemical stimuli are transported in very small amounts. Some of them are transported in polarised or unidirectional manner while others diffuse to all parts. Therefore, a complex traffic of materials is going on in flowering plants, some moving to different directions, some passing out in polarised manner, with most organs receiving some substances and giving out some others.

Means of Transport

Passage of materials into and out of the cells is carried out by a number of methods—

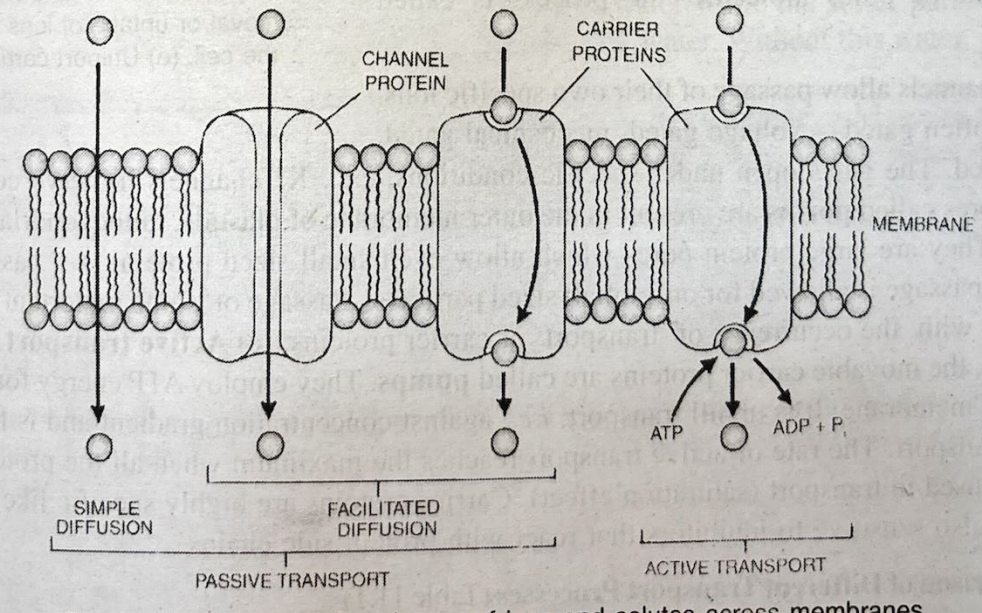


Fig. 11.1. Three ways of exchange of ions and solutes across membranes.

diffusion, facilitated diffusion, active transport. (a) **Diffusion**. Movement by **diffusion** is passive and slow. It occurs along the concentration gradient, *i.e.*, from region of higher concentration to region of lower concentration provided the cell membrane is permeable to it. No energy expenditure takes place. (b) **Facilitated Diffusion**. Particles which are lipid soluble can easily pass directly through the cell membrane as it is mainly made of it. The hydrophilic solutes, find it difficult to pass through the membrane. Their movement has to be facilitated. For this the membranes possess aquaporins and ion channels. Eight different types of **aquaporins** or water channels have been recorded. Aquaporins are membrane proteins for passive transport of water soluble substance. They do not set up a concentration gradient. No energy is utilized. The diffusion of hydrophilic substances along the concentration gradient through fixed membrane transport protein without involving energy expenditure, is called **facilitated diffusion**. This diffusion is very specific as it allows cell to select substances for uptake. It is sensitive to inhibitors as well as show saturation effect. Two major types of transport proteins are known *viz.*, **carrier proteins** (also called carriers, transporters) and **channel proteins**. Carrier proteins bind the particular solute to be transported and deliver the same to the other side of the membrane. Channel proteins allow diffusion of the solutes of an appropriate size may diffuse. Some carrier proteins allow transport only if two types of molecules move together. This is called **cotransport**. It is of two types (Fig. 11.2). In **symport** method of **cotransport**, both molecules cross the membrane in the same direction at the same time. In **antiport** method of cotransport, both molecules move in opposite direction. When a molecule moves accross a membrane independent of other molecule, the process is called **uniport**.

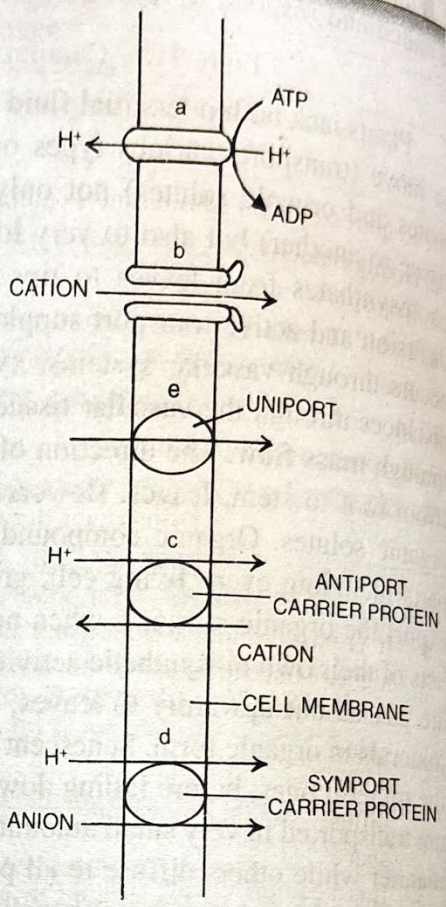


Fig. 11.2. Diagram showing activity of a membrane proton pump to solute exchange. (a) Proton pump using ATP to establish a proton gradient. (b) Ion channel activated by proton gradient. (c) Antiport carrier and (d) Symport carrier to drive the removal or uptake of ions from the cell. (e) Uniport carrier.

Ion channels allow passage of their own specific ions. They are often gated— voltage gated, mechanical gated, ligand gated. The gates open under specific conditions, *e.g.*, K^+ channels in nerve conduction. Certain pores called **porins** are present in the outer membrane of plastids, mitochondria and some bacteria. They are large protein pores which allow even small sized proteins to pass through. Normally passage is allowed for only small sized particles. Passage of some important solutes is connected with the occurrence of transport or carrier proteins. (c) **Active transport**. In **active transport**, the movable carrier proteins are called **pumps**. They employ ATP energy for transport across the membrane. It is uphill transport, *i.e.*, against concentration gradient and is faster than passive transport. The rate of active transport reaches the maximum when all the protein pumps are being used in transport (saturation effect). Carrier proteins are highly specific like enzymes. They are also sensitive to inhibitors that react with protein side chains.

Comparison of Different Transport Processes (Table 11.1)

Simple diffusion does not require the assistance of proteins for passage through the mem-

brane. Both facilitated diffusion and active transport are mediated through membrane proteins. Active transport requires ATP energy. It is also uphill transport. Facilitated transport does not require ATP energy. It usually occurs along the concentration gradient. The protein transporters of both facilitated diffusion and active transport are highly selective. They are liable to get saturated and respond to inhibitors as well as hormonal regulation.

Table 11.1. Comparison of Different Transport Mechanisms

Property	*Simple Diffusion*	*Facilitated Transport*	*Active Transport*
1. Requires Special Membrane Proteins	No	Yes	Yes
2. Highly Selective	No	Yes	Yes
3. Transport Saturates	No	Yes	Yes
4. Uphill Transport	No	No	Yes
5. Requires ATP Energy	No	No	Yes
6. Movement of Transport Proteins	No	No	Yes
7. Response to protein inhibitors	No	Yes	Yes

Differences between Diffusion and Facilitated Diffusion

Diffusion	*Facilitated Diffusion*
1. It is passage of particles from the area of higher concentration to the area of lower concentration, throughout the available space.	1. It is passage of particles from the area of higher concentration to the area of lower concentration through specific sites.
2. A number of different types of particles can diffuse simultaneously through the same space.	2. Only one type of particles can pass through its specific sites in facilitated diffusion.
3. It is a completely physical process.	3. It is a physical process that is dependent upon the availability of specific sites.

PLANT-WATER RELATIONS

Water is a major component of all living cells, a medium in which all substances are dissolved and undergo various types of reactions. Water is itself a reactant as well as a product. Most herbaceous plants contain 85–90% water while Water Melon has 92% water. In trees and shrubs the woody parts have relatively lower amount of water while the softer parts have quite a large amount of it. A seed which appears dry has 10–15% water. Without this water, it will stop respiring and die.

The amount of water absorbed by a plant is very high. For example, a Maize or Corn plant absorbs about 3 litres of water per day while a Mustard plant would absorb water equal to its weight in just five hours. The amount of water absorbed by larger sized plants is very large, 36–45 litres in Apple and more than 1 tonne per day in Elm tree. Because of this huge requirement of water, it is often a limiting factor for plant growth and productivity both in agriculture and natural ecosystems.

IMBIBITION

The absorption of water by the solid particles of an adsorbent causing it to enormously increase in volume without forming a solution is called **imbibition**. Solid substances or adsorbents which take part in imbibition are called **imbibants**, *e.g.*, seeds, dry wood. The liquid (usually water) which is imbibed is known as **imbibate**. The imbibate is held in between and over the surface of particles of the solid substance through the processes of **capillarity** and **adsorption**. Plant imbibants are **hydrophilic** (Gk. *hydor*— water, *philein*— to love) colloids. They have a highly negative water potential. As a result when they come in contact with water (ψ_w = O), a steep water potential gradient is established. Water diffuses rapidly into the adsorbent. The

process will continue till an equilibrium is established. Amount of imbibition depends upon (i) Water potential gradient between adsorbent and water and (ii) Affinity of adsorbant for water. Imbibition increases the volume of the imbibant but the increase is less than the volume of water absorbed. It is caused by holding of water in between and over the surface of imbibant particles. Water molecules are immobilised. Their kinetic energy is released in the form of heat (**heat of wetting**). The swelling imbibant also develops a pressure called **imbibition pressure** (matric potential). Air dried Pea seeds on coming in contact with water can develop an imbibition pressure of upto 1000 bars (= 100 MPa). This is tested by placing dry seeds in a tin, adding water upto their upper level and then tightly putting the lid over it. Within an hour the lid will be blown off. Alternately fill a gas jar ¾ with dry seeds. Pour water upto the brim. Cover the cylinder with lid and place a weight over the lid. Within a couple of hours the lid alongwith weight is lifted. Imbibition capacity is maximum in phycocolloids followed by proteins, starch and cellulose. Lignin is **hydrophobic**. It, therefore, does not show imbibition of water. Imbibition is influenced by a number of factors like texture (looseness more and compactness less imbibition) of the imbibant, temperature (rises with rise of temperature), pressure (decreases if pressure is against imbibant), electrolytes (decreases) and *p*H (decreases or increases depending upon charge of imbibant).

Imbibition plays an important role in absorbing and retaining water. (i) Absorption of water by young cells is mostly through imbibition. (ii) Water is absorbed by the germinating seeds through imbibition. (iii) Breaking of the seed coat in germinating seeds is due to greater imbibitional swelling of the seed kernel (starch and protein) as compared to seed coverings (cellulose). (iv) Seedling is able to come out of soil due to development of imbibition pressure. (v) Imbibition pressure developed during germination of seeds and spores can break asphalt roads and concrete pavements. (vi) Jamming of wooden frames during rains is caused by swelling of wood due to imbibition. (vii) In older times, it was used in breaking the rocks and boulders. Wooden pegs were inserted in rocks. They were then made wet. As a consequence the wooden pegs developed huge imbibition pressures that could break the rocks into pieces. (viii) Fruits of many plants come to develop matric potential in addition to their osmotic potential in order to maintain inflow of water even under conditions of water scarcity.

DIFFUSION

The tendency on the part of molecules, atoms, ions, etc., of gases, liquids and solids to get evenly distributed throughout the available space on account of their **random kinetic motion** is called diffusion. Random kinetic motion of particles is due to kinetic energy present in them. Diffusion is also defined as the movement of the particles of different substances from the region of their higher concentration, free energy or diffusion pressure to region of their low concentration, free energy or diffusion pressure. Diffusion is dependent upon the number of particles per unit volume, density of medium, distance through which diffusion is to occur, temperature and pressure. Diffusion will be more rapid when the difference in concentration is larger. Gases diffuse more rapidly than liquids. Solids are the slowest to diffuse. When the particles of diffusing substance get evenly distributed, a state of equilibrium is reached. It stops further movement.

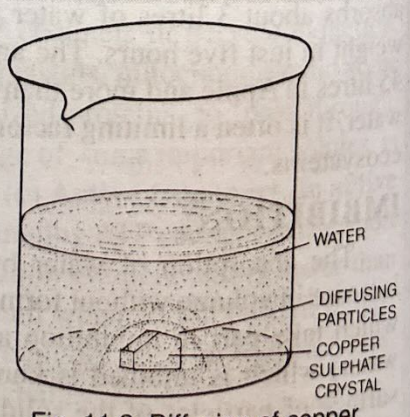


Fig. 11.3. Diffusion of copper sulphate from crystal in a beaker containing water.

Diffusion of particles of one substance is independent of the diffusion of particles of another substance, provided the two do not react. It is known as **independent diffusion**. The diffusion pressure of the individual substance is then known as **partial pressure**. Thus in photosynthesising leaf, water vapours and oxygen diffuse out while carbon dioxide enters the leaf depending upon the differences in their partial pressures in the leaf interior and the outside. Diffusion is also responsible for uptake and distribution of water and solutes.

(i) Open a bottle of perfume in one corner of room. Soon odour of the perfume will be felt throughout the

room. (ii) Place a **crystal** of **copper sulphate** in a beaker containing **water**. An intense blue colour will be seen around the crystal. It decreases with the increase of distance from the crystal. It shows that copper sulphate molecules are diffusing into water (Fig. 11.3). Water molecules will also move towards copper sulphate crystal in order to occupy that space. Ultimately the molecules of the two, water and copper sulphate, will be evenly distributed throughout the solution.

Diffusion Pressure (D.P.). The pressure exerted by the tendency of the particles to diffuse from the area of its higher concentration to the region of its lower concentration is called diffusion pressure. It is proportional to the concentration of diffusing particles. A porous pot is fitted to a glass tube, one end of which dips in water. A gas jar filled with hydrogen is inverted over the porous pot. Hydrogen has the ability to diffuse more rapidly into porous pot than the ability of air to diffuse out of the porous pot. This develops a pressure inside the porous pot which pushes the air from the tip of glass tube into water in the form of air bubbles (Fig. 11.4).

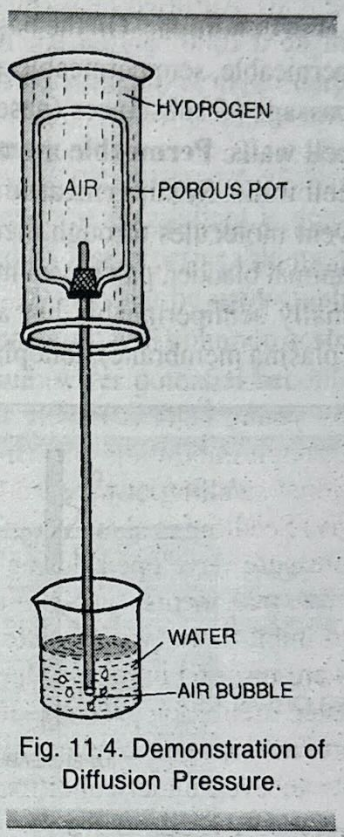


Fig. 11.4. Demonstration of Diffusion Pressure.

Factors Influencing Diffusion. (i) **Density**. Rate of diffusion of a substance is inversely proportional to square root of its relative density (Graham's Law). (ii) **Permeability of Medium**. Rate of diffusion decreases with density of the medium. (iii) **Temperature**. A rise in temperature increases the rate of diffusion with Q_{10} = 1·2–1·3. Because of it sugar crystals do not dissolve easily in ice cold water while they do so easily in warm water. (iv) **Diffusion Pressure Gradient**. Rate of diffusion is directly proportional to the difference of diffusion pressure at the two ends of a system and inversely proportional to the distance between the two.

Importance. (i) Diffusion keeps the cell walls of the internal plant tissues moist. (ii) It is a means of spreading of ions and other substances throughout the protoplast. (iii) Transpiration or loss of water in vapour forms is a diffusion process. (iv) Exchange of gases (CO_2 and O_2) between the plant interior and outside air occurs through diffusion. (v) Osmosis is a special type of diffusion in which water diffuses through a semi-permeable membrane. (vi) Aroma of flowers is due to diffusion of volatile aromatic compounds to attract pollinating animals.

Differences between Diffusion and Imbibition

Diffusion	*Imbibition*
1. It is movement of substances from the region of their higher concentration to the region of lower concentration.	1. It is absorption of water by the particles of a solid without forming a solution.
2. An adsorbent is absent.	2. Imbibition only occurs when an adsorbent (=imbibant) is present.
3. All the substances present in the medium show diffusion.	3. Only the liquid diffuses. The solid particles do not diffuse.
4. There is little change in pressure.	4. A very high pressure develops on imbibition
5. Energy is not liberated.	5. Heat is liberated during imbibition.
6. There is no change in volume.	6. The imbibant swells up but the swelling is less than volume of imbibate.

Membrane Permeability

Membrane permeability is the ability of a membrane to allow passage of gases, liquids, solutes (dissolved substances) through it. It is dependent upon two factors—nature of membrane (membrane composition) and nature of passing substance. Permeability of a membrane is measured by determining the rate of passage of a substance through it under specific standard set of conditions. On the basis of their permeability, membranes are of four types — impermeable, permeable, semipermeable and selectively permeable. **Impermeable membranes** do not allow the passage of substances (gases, solvent, solute) through them, *e.g.*, suberised cell walls, cutinised cell walls. **Permeable membranes** allow the passage of substances through them, *e.g.*, cellulose cell walls. **Semipermeable membranes** are those membranes which permit the movement of solvent molecules through them but prevent the movement of solute particles, *e.g.*, egg membrane, animal bladder, parchment membrane. Selectively or **differentially permeable membranes** are normally semipermeable but allow selective passage of solutes through them, *e.g.*, plasmalemma (plasma membrane), tonoplast.

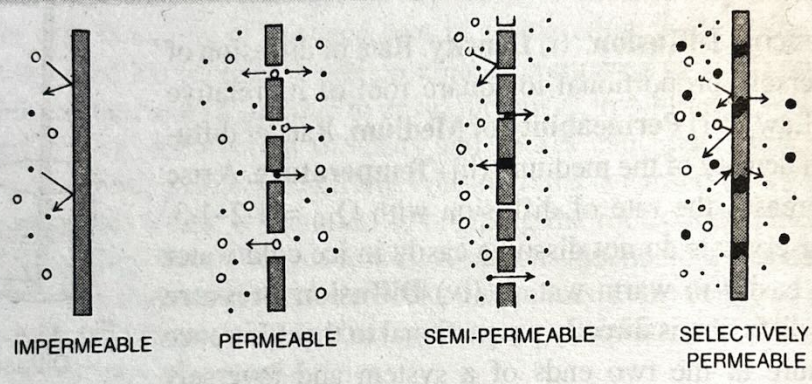


Fig. 11.5. Types of membranes on the basis of their permeability.

Differences between Semipermeable and Selectively Permeable Membranes

Semipermeable Membrane	*Selectively Permeable Membrane*
1. It does not allow passage of solutes through it.	1. It allows passage of some selected solutes to a limited extent.
2. It forms a perfect partition between two osmotically active solutions or between a solution and its pure solvent.	2. The partition is imperfect because of which even plasmolysed protoplasts get deplasmolysed automatically even when kept in the same hypertonic solution.
3. It allows entry of only solvent.	3. It allows entry of both solvent and to a selected extent solutes.
4. It is not found in biological world, *e.g.*, collodion, cellophane.	4. Almost all biological membranes are selectively permeable.
5. Semipermeable, membrane is used in dialysis, maintenance of turgidity and measurement of osmotic potential.	5. Selectively permeable membrane is useful in maintaining turgidity while retaining the ability to absorb solutes.

OSMOSIS

Osmosis is a special type of diffusion of water that occurs through a semipermeable membrane.

Definition of Osmosis. (i) Diffusion of water from its pure state or dilute solution into a

solution or stronger solution when the two are separated by a semipermeable membrane is termed as osmosis.

(ii) The movement of water from its higher chemical potential (found in pure state or dilute solution) to its lower chemical potential (found in solution or stronger solution) without allowing the diffusion of solute by means of a semipermeable membrane is called osmosis. The chemical potential of water is also called **water potential.**

(iii) Osmosis is movement of solvent or water molecules from the region of their higher diffusion pressure or free energy to the region of their lower diffusion pressure or free energy across a semipermeable membrane.

The direction and rate of osmosis depend upon the sum of two forces, pressure gradient (gradient of Ψ_p) and concentration gradient (gradient of Ψ_s). The net force or gradient is determined by the difference in the water potentials of solutions separated by a semipermeable membrane. A solution which can cause an osmotic entry of water into it is said to be **osmotically active solution**. It possesses a low water potential. Diffusion of water into it will continue across the separating membrane till an equilibrium is reached. At equilibrium water potential becomes equal on both sides of the membrane.

Explanation. Solute particles decrease the chemical potential of water by decreasing the mole fraction of water. In osmosis, a semipermeable membrane separates (say) dilute solution A and concentrated solution B. Solute particles cannot pass through the semipermeable membrane. Water molecules are in random motion. They strike the semipermeable membrane on both the sides and pass through the same (Fig. 11.6). Since more free water molecules are present on the side of dilute solution A, more of them pass through the membrane to enter the solution B as compared to the reverse flow. There is, therefore, a net diffusion of water from its higher chemical potential (dilute potential) to its lower chemical potential (concentrated solution).

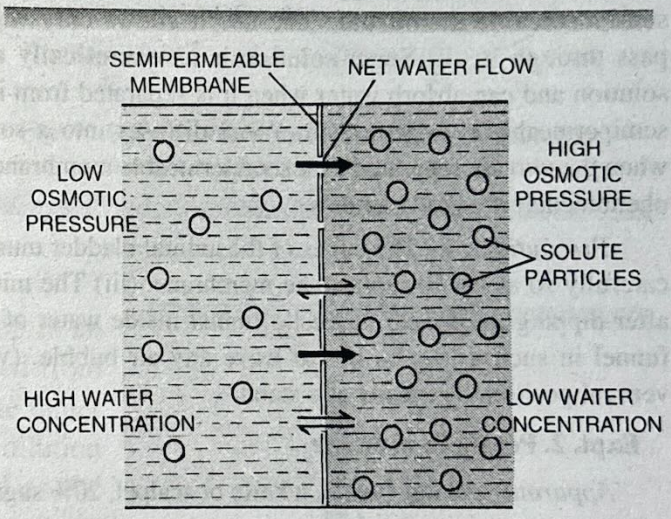


Fig. 11.6. Net movement of water from its higher chemical potential (dilute solution) to lower chemical potential (concentrated solution) when the two are separated by a semipermeable membrane.

Types of Osmosis. Osmosis is of two types— (i) **endosmosis**— the osmotic entry of water into a cell, organ or system (ii) **exosmosis**— the osmotic withdrawal of water from a cell, organ or system.

Demonstration of Osmosis

Expt. 1. Thistle Funnel Experiment

Apparatus. 10% sugar solution, a long stemmed thistle funnel, animal bladder, egg membrane or parchment paper, thread, scissors, rubber solution, beaker, water, glass marking pencil or gummed paper and stand. Egg membrane is prepared by first removing the yolk and albumin of the egg through a small hole at one end. The egg shell with membrane is then placed in dilute hydrochloric acid for a few hours when the shell will dissolve. The egg membrane is left intact.

Working. Take a thistle funnel having a long stem. Close the mouth of the funnel with a membrane of animal bladder or parchment paper by means of thread. Remove the free edges of the membrane with the

help of scissors as close to thread as possible. The terminal edges of the membrane are then sealed by applying rubber solution. This makes the joint water tight.

Pour 10% sugar solution in the thistle funnel till it stands at about 1/3 of the height of the stem. Now dip the covered end of the thistle funnel in a beaker containing water (Fig. 11.7). Support it in its position by means of a stand. Mark the level of sugar solution as A by means of glass marking pencil or gummed paper. Note that after a few minutes the level of the sugar solution has risen in the stem of thistle funnel to a point B while the level of water falls down in the beaker. Taste the water of the beaker. It is not sweet.

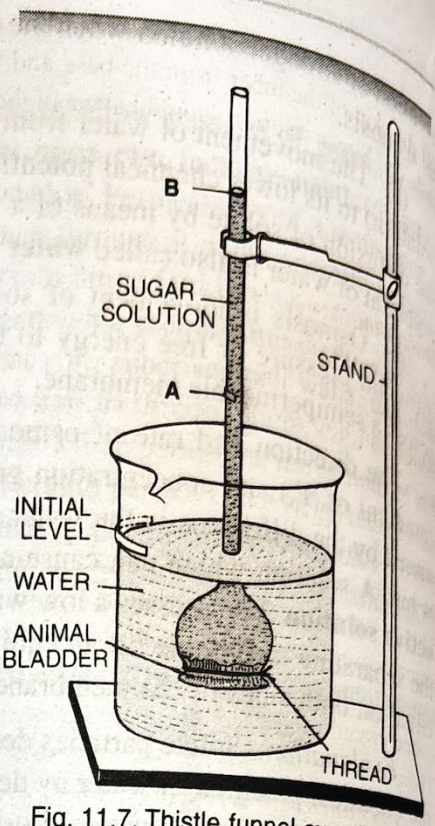


Fig. 11.7. Thistle funnel experiment to demonstrate osmosis.

Results. The rise of sugar solution in thistle funnel can only be due to the entry of water into it through the animal bladder. But no sugar has gone out into the water of the beaker as it does not taste sweet. The experiment, therefore, proves that :

(i) Animal bladder, egg membrane or parchment paper is a **semipermeable membrane** because it allows only water to pass through it. (ii) Sugar solution is an **osmotically active** solution and can absorb water when it is separated from it by a semipermeable membrane. (iii) Water diffuses into a solution when the two are separated by a semipermeable membrane. The phenomenon is called **osmosis**.

Precautions. (i) The edges of the animal bladder must be properly sealed. (ii) The thread should be tied carefully so as not to rupture the membrane. (iii) The initial level of sugar solution should be marked only after dipping the mouth of thistle funnel inside water of the beaker. (iv) Pour sugar solution in the thistle funnel in such a way as not to leave any air bubble. (v) Support and fix the thistle funnel firmly in its vertical position by means of a stand.

Expt. 2. Potato Osmoscope

Apparatus. A large potato, a knife or scalpel, 20% sugar solution, petri dish containing water, two pins.

Working. Take a large sized potato tuber. Cut one side of it so as to make it flat. Bore a cavity from the other side in such a way that a very thin base is left intact on the flat side. Also remove the skin near the edge of the flat end because skin of the tuber is impermeable to water.

Pour 20% sugar solution in the cavity of the tuber up to ½ – ¾. Mark the level of sugar solution in the cavity with the help of a pin (Fig. 11.8 A). Place the tuber on its flat cut end in a petri dish half full of water. Note that after some time the level of the sugar solution has risen in the cavity. Mark this reading also with another pin (Fig. 11.8 B).

Results. The rise in the level of sugar solution in the cavity of the potato tuber indicates that the solution has absorbed water from the petri dish. The two are separated from each other by a large number of cells of the tuber. The entry of water into the sugar solution, therefore, proves that : (i) Sugar solution is **osmotically active** solution. (ii) The cytoplasm of the cells of the tuber that lie between the sugar solution and the water of the petri dish act as a single **semipermeable membrane**. (iii) Water enters the sugar solution when it is separated from it by semi-permeable membrane. This process is called **osmosis**.

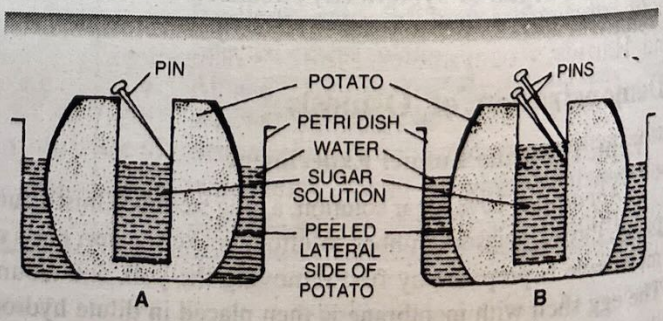


Fig. 11.8. Potato osmoscope experiment to demonstrate osmosis. A, Original level; B, Final level.

Precautions. (i) The cavity should be deep so as to leave only a thin layer of tissue at the base. (ii) Peel off the skin of the tuber from the base and the sides. (iii) Make the base flat so as to keep the tuber flat in the dish. (iv) Sugar solution should have a higher osmotic concentration as compared to cell sap of the tuber cells.

Expt. 3. Demonstration of Endomosis and Exosmosis

Apparatus. A few grapes and raisins with intact stalks, water, 10% salt solution, petri dishes.

Place a few raisins in water for about 5–6 hours. Raisins will swell up. The swelling can be due to the absorption of water from the petridish.

In another petri dish place a few fresh grapes, (or swollen raisins) and pour 10% salt solution into the dish. After a few hours the grapes will shrivel which can be possible only when they have lost water to the salt solution (Fig. 11.9).

In the first case the raisins have absorbed water from the outside due to the presence of higher concentration of solute in them. This is an example of **endosmosis**. In the second case, the grapes have lost water to the salt solution because salt solution is more concentrated than the sap present in grapes. Therefore, it is an example of **exosmosis**.

Precautions. (i) Grapes and raisins should be with intact stalks. (ii) The solution for exosmosis must be stronger than sap concentration of grapes.

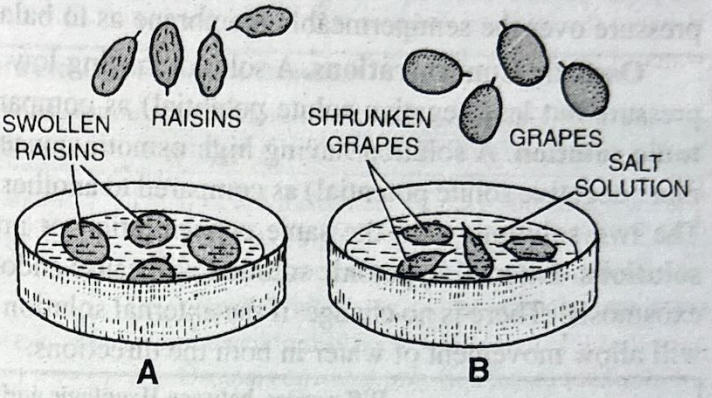


Fig. 11.9. Experiment to demonstrate endosmosis in raisins and exosmosis in grapes.

Osmotic Pressure (O. P.)

It is maximum pressure which can develop in an osmotically active solution when it is separated from its pure solvent by a semipermeable membrane under ideal conditions of osmosis that do not allow dilution of solution. Osmotic pressure is also defined as the pressure required to completely stop the entry of water into an osmotically active solution across a semipermeable membrane (Fig. 11.10). It is measured in atmospheres, bars or pascals*. Osmotic pressure is numerically equal to osmotic potential (= solute, potential, ψ_s) but while osmotic potential has a negative value, osmotic pressure (π, pi) has a positive value, ($\psi_s = -\pi$). The instrument used for measuring osmotic pressure is called **osmometer**, *e.g.*, Berkeley and Hartley's osmometer, Pfeffer's osmometer.

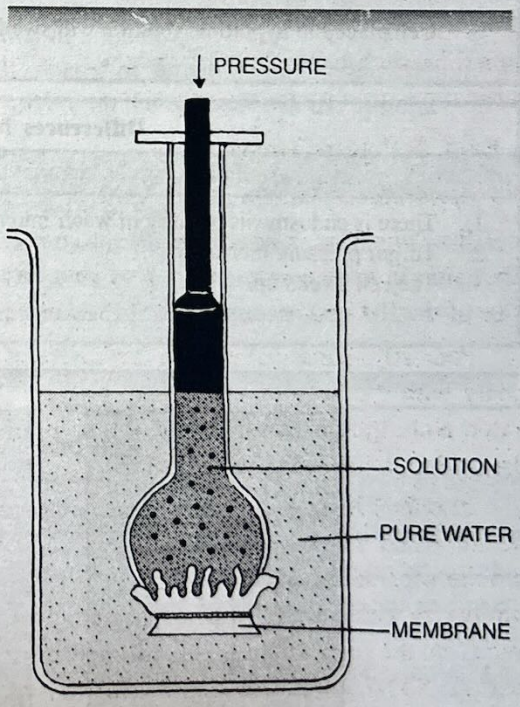


Fig. 11.10. Measurement of osmotic pressure of a solution.

Aquatic plants have an osmotic pressure of 1–3 atm, mesophytes 5–15 atm while in xerophytes it lies between 10–30 atm but goes upto 60 atm under drought conditions. Upper leaves have more osmotic pressure than the lower leaves. Seeds may develop an osmotic pressure of 100 atm. Halophytes have the maximum osmotic pressure with *Atriplex confertifolia* showing an O.P. of 202. 4 atm (Harris, 1934).

* 1 bar = 0.987 atm = 10^5 pascals (Pa) = 0.1 Megapascal (MPa).

Reverse Osmosis. It is the expulsion of pure water from a solution through a semipermeable membrane under the influence of pressure higher than the O.P. of the solution. Reverse osmosis is used in removing salts from saline water as well as extra-purification of water.

Factors Controlling Osmosis. Presence of a perfectly semipermeable membrane is a must for the operation of osmosis. Osmosis is driven by two other factors; (i) Concentration of dissolved solute on the two sides of semipermeable membrane. (ii) Difference in pressure. In thistle funnel experiment there is no indefinite passage of water from beaker into the funnel despite the fact that osmotic potential of the solution continues to be negative as compared to the chemical potential of pure water. It is because after some distance the raised column of solution exerts sufficient pressure over the semipermeable membrane as to balance the chemical potential of pure water.

Osmotic Concentrations. A solution having low osmotic concentration (hence low osmotic pressure but less negative solute potential) as compared to another solution is known as **hypotonic solution**. A solution having high osmotic concentration (hence high osmotic pressure but more negative solute potential) as compared to another solution is termed as **hypertonic solution**. The two solutions with the same concentration or pressure or potential are named as **isotonic solutions**. External hypotonic solution will cause endosmosis while hypertonic solution results in exosmosis. There is no change if the external solution is isotonic (Fig. 11.11). Such a **flaccid** cell will allow movement of water in both the directions.

Differences between Hypotonic and Hypertonic Solutions

Hypotonic Solution	*Hypertonic Solution*
1. It is a solution which is more dilute as compared to another solution.	1. It is a solution which is more concentrated as compared to another solution.
2. The osmotic potential is higher, *i.e.*, less negative.	2. The osmotic potential is lower, *i.e.*, more negative.
3. Cell placed in hypotonic solution will swell up.	3. Cells placed in hypertonic solution will undergo plasmolysis.

Differences between Turgid and Flaccid Cells

Turgid Cell	*Flaccid Cell*
1. There is endosmosis or entry of water into a cell.	1. The cell does not undergo endosmosis.
2. Turgor pressure increases.	2. There is no increase in turgor pressure.
3. The cell swells up.	3. There is no swelling as equal amounts of water pass in and pass out of the cell.

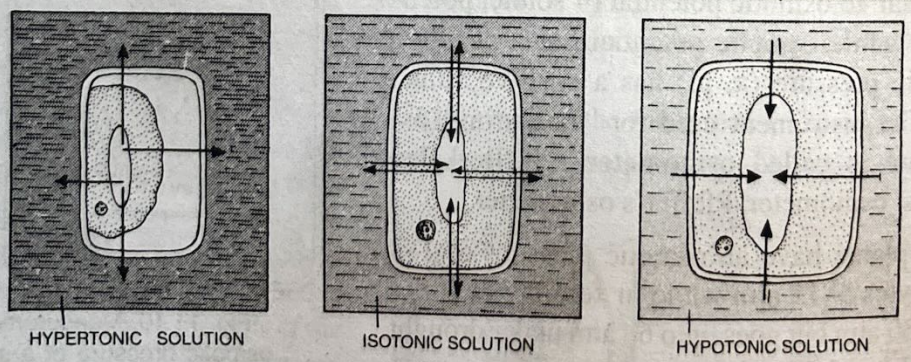


Fig. 11.11. Behaviour of a living cell placed in solutions of different concentrations.

Importance of Osmosis

(1) Entry of soil water into root is carried out by osmosis. (2) Osmosis performs cell to cell movement of water. (3) Living cells remain distended or turgid only by the osmotic entry of water into them. (4) Various cell organelles like mitochondria and chloroplasts will collapse if they are

not able to maintain a proper osmotic concentration. (5) 70% of cell water is held in vacuoles. It has come from outside through endosmosis and is kept in its place due to osmotic concentration of solutes dissolved in it. (6) The soft organs like leaves, flowers, fruits and young stems are able to keep themselves stretched and swollen due to turgidity of their cells which is dependent upon osmosis. (7) Osmosis plays a key role in the growth of radicle and plumule during the germination of seeds. (8) Many plant movements like the folding and drooping of leaves in *Mimosa* are brought about by osmosis. (9) The stomata open and close only in response to increase or decrease of the osmotic pressure of the guard cells in relation to nearby epidermal cells. (10) A high osmotic pressure has been found to protect the plants against drought and frost injury. Seeds and spores are similarly able to pass through the unfavourable periods due to high osmotic pressure (or low solute potential).

Differences between Diffusion and Osmosis

Diffusion	*Osmosis*
1. It is the movement of all types of substances from the area of their higher free energy to the area of their lower free energy.	1. It is the movement of only solvent or water from its higher free energy or chemical potential to the area of its lower chemical potential when the solute particles are not allowed to diffuse.
2. Diffusion can operate in any medium.	2. Osmosis operates only in a liquid medium.
3. Diffusion is applicable to all types of substances— solids, liquids or gases.	3. It is applicable to only solvent part of a solution.
4. It does not require any semipermeable membrane.	4. A semipermeable membrane is a must for the operation of osmosis.
5. It is purely dependent upon the free energy of the diffusing substance.	5. Osmosis is dependent upon the degree of reduction of free energy of one solvent over that of another.
6. It helps in equalising the concentration of the diffusing substance throughout the available space.	6. It does not equalise the concentration of solvent on the two sides of the system.
7. Hydrostatic or turgor pressure does not normally operate in diffusion.	7. Osmosis is opposed by turgor or hydrostatic pressure of the system.
8. It is not influenced by solute potential.	8. Osmosis is dependent upon solute potential.
9. Diffusion of a substance is largely independent of the presence of other substances.	9. Osmosis is dependent upon the number of particles of other substances dissolved in liquid.

Differences between Imbibition and Osmosis

Imbibition	*Osmosis*
1. It involves the absorption of solvent or water by a solid substance.	1. It involves the movement of water or solvent from its higher chemical potential to lower chemical potential.
2. A semi-permeable membrane is not required.	2. A semi-permeable membrane is essential for the operation of osmosis.
3. Imbibition does not produce a solution.	3. Osmosis usually operates in solutions separated by semipermeable membrane.
4. It produces heat.	4. Heat is not produced.
5. It can develop a very high pressure (upto 1000 atm) called imbibition pressure.	5. Osmosis develops a comparatively lower pressure (upto 100 atm) known as osmotic pressure.
6. Imbibition requires the presence of colloidal particles.	6. Osmosis usually requires the presence of solute particles.

Diffusion Pressure Deficit (DPD; Meyer, 1938)

It is an older term that was used in place of water potential. Pure water has the **maximum diffusion pressure**. Its diffusion pressure gets lowered by the addition of solute particles in it. *The reduction in the diffusion pressure of water in a solution over its pure state is called diffusion pressure deficit* or DPD. Because of the presence of diffusion pressure deficit, a solution will always tend to make up the deficit by absorbing water. Diffusion pressure deficit is also called **suction pressure**. Its value is equal to the osmotic pressure or potential (positive value taken in bars or atm) of the solution in a cell or system minus the wall pressure (= turgor pressure) which opposes the entry of water into it provided the external water is pure.

$$DPD = OP - WP\ (= TP)$$

In case the external fluid is a solution the value of DPD will be equal to the difference in osmotic pressures of cell solution (OP_1) and external solution (OP_2) minus the wall pressure.

$$DPD = (OP_1 - OP_2) - WP\ (= TP)$$

WATER POTENTIAL (Slatyer and Taylor, 1960)

It is the difference in the free energy or chemical potential per unit molal volume of water in a system and that of pure water at the same temperature and pressure. Chemical potential of pure water at normal temperature and pressure is zero. In solutions the value of water potential is always negative or less than zero. It is represented by greek letter ψ(psi) or more accurately ψ_w. The value of ψ_w is measured in bars, pascals or atmospheres. Water always moves from the area of high water potential or high energy to the area of low water potential or low energy, *i.e.*, from less negative potential (*e.g.*, –1000 KPa) to more negative potential (*e.g.*, –2000 KPa). If two systems having water are in contact, more random movement of water molecules in the system having higher water potential or more energy will result in their net movement towards the system with low energy or low water potential, *e.g.*, soil and air, cell and solution. The movement of a substance from an area of higher free energy to area of lower free energy is called **diffusion**.

Water potential or ψ_w is the sum total of ψ_s and ψ_p.

$$\psi_w = \psi_s + \psi_p$$

ψ_s designates the effect of solute on the free energy of water while ψ_p indicates the effect of pressure on the same. However, another force which has a negative value and which decreases the water potential is matric potential (ψ_m). It is reduction in free energy of water when the latter comes to form thin surface layers adsorbed over colloidal particles. It is appreciable in case of dry seeds, young cells and dry soils. However, in case of mature cells and hydrated cell walls the effect of matric potential is negligible.

Differences between Diffusion Pressure Deficit (DPD) and Water Potential (Ψw)

Diffusion Pressure Deficit (DPD)	*Water Potential (Ψw)*
1. It is an old term coined by Meyer (1938) which is synonym with water potential.	1. It is modern term coined by Slatyer and Taylor (1960) which is equivalent to DPD.
2. It has positive value, *e.g.*, 5 atm.	2. It has a negative value *e.g.*, –5 atm.
3. Diffusion pressure deficit is the reduction in diffusion pressure of solvent in a system over its pure state.	3. Water potential is reduction in free energy of solvent in a system over its pure state.
4. Water is absorbed by a system having higher DPD from another system with lower DPD.	4. Water is absorbed by a system with lower Ψw from another system with higher Ψw.

5. DPD = OP – TP where all the terms are with positive values. 6. Matric pressure or imbibitional force is not considered.	5. $\Psi w = \Psi s + \Psi p$ where Ψs has a negative value while Ψp has a positive value. 6. Matric potential or Ψm is considered wherever it is appreciable.

Osmotic or Solute Potential (ψ_s). It is the decrease in the chemical potential of pure water due to the presence of solute particles in it. It is a colligative property of solute and is dependent upon the number of solute particles and not upon the nature of solute. Solute particles reduce the free energy of water by diluting it, increasing entropy, reducing vapour pressure, raising boiling point and lowering freezing point. Its value is calculated by the following formula

$$OP \text{ or } SP = C \times R \times T$$

where C is the concentration of solute particles in moles per litre (one mole or molecular weight in grams = 6.02×10^{23} particles or molecules), R is gas constant with a value of 0.083 (0.082 if in atmospheres) and T is the temperature in absolute degrees.

Thus osmotic potential of a molar solution of a nonelectrolyte like sucrose at 0°C or 273°A and 20°C or 293°A can be calculated as below :

at 0°C = $1 \times 0.083 \times 273$ = 22.7 bars or 22.4 atm (as negative)

at 20°C = $1 \times 0.083 \times 293$ = 24.3 bars or 24 atm. (as negative)

In case of electrolytes, the degree of ionisation is taken into consideration because osmotic or solute potential depends upon the number of particles (here as ions and molecules) and not upon the number of molecules alone. In case of strong electrolytes the osmotic potential may be almost double or triple as compared to nonelectrolytes. For example, 0.1N sucrose solution has an osmotic potential of –2.3 bars while 0.1N sodium chloride solution has ψ_s value of –4.5 bars.

Differences between Osmotic Pressure and Osmotic Potential

Osmotic Pressure	*Osmotic Potential*
1. It is the pressure which develops in an osmotic system due to entry of water into it.	1. It is lowering of free energy of water in a system due to the presence of solute particles.
2. It develops only in a confined system.	2. Osmotic potential is present whether the solution occurs in a confined system or an open system.
3. The value is positive though numerically equal to osmotic potential.	3. The value is negative though it is numerically equal to osmotic pressure.

Differences between Osmotic Potential and Matric Potential

Osmotic Potential	*Matric Potential*
1. It is reduction in free energy of water due to decrease in number of water molecules per molal volume.	1. It is reduction in free energy of water due to formation of thin immobile surface layers of water molecules.
2. Osmotic potential is caused by the presence of solute particles.	2. Matric potential is caused by adsorbant or colloidal particles.
3. It is important in water relations of plant cells.	3. It is unimportant in water relations of mature plant cells though essential for seed germination, early seedling growth and growth of developing fruits.
4. The value is rarely more than 0.5 – 2.0 MPa.	4. The value is 50 – 200 MPa.

Pressure Potential (ψ_p) or Hydrostatic Pressure

It is the pressure which develops in an osmotic system due to osmotic entry or exit of water from it. A positive pressure develops in a plant cell or system due to entry of water into it. Positive hydrostatic pressure is also called **turgor pressure**. Loss of water produces a **negative hydrostatic pressure** or **tension**. It develops in xylem due to loss of water in transpiration. This is very important in transport of sap over long distances in plants.

Positive hydrostatic pressure or *turgor pressure is the pressure which develops in the confined part of an osmotic system due to osmotic entry of water into it.* Due to turgor pressure the protoplast of a plant cell will press the cell wall to the outside. The cell wall, being elastic, presses the protoplast with an equal and opposite force. *The force exerted by the cell wall over the protoplast is called wall pressure* (WP). Normally wall pressure is equal and opposite to turgor pressure except when the cell becomes flaccid. The values of these two opposing forces continue to rise till the cell becomes fully swollen or **turgid**. At this time the value of wall or turgor pressure becomes equal to osmotic potential, $\psi_p = \psi_s$.

Turgor pressure has number of important functions :

(i) It keeps the cells and their organelles stretched. This is essential for proper functioning of a cell.

(ii) It provides support to nonwoody tissues like parenchyma.

(iii) Turgor pressure is essential for cell enlargement during growth.

(iv) It keeps the leaves fully expanded and properly oriented to light. Flowers, young stems and other softer organs are able to maintain their form due to turgidity or TP. In case of loss of turgidity, the shoots droop down and the leaves show wilting. Wilting is observed in many plants during summer noon. In wilting the individual cells of leaves and other softer parts become flaccid due to loss of water from their interior. Plants gain their turgidity during night because of continued absorption of water from the soil. If the soil does not obtain water periodically (*i.e.*, the soil is deficient in water), the recovery may be only partial or it may not occur at all. The latter condition is known as **permanent wilting**. The plants are soon killed. Temporary wilting reduces growth and decreases the yield of plant.

(v) Many plant movements are produced due to reversible turgor changes in the cells. Sleep movements (nyctinasty) of bean leaves and shock movements (seismonasty) of Sensitive Plant (*Mimosa pudica*) are produced due to turgor changes in the cells of their pulvini. Regular turgor changes in the leaflet bases cause rhythmic autonomic jerky movements in the lateral leaflets of Indian Telegraph Plant, *Desmodium gyrans* (Fig. 11.12).

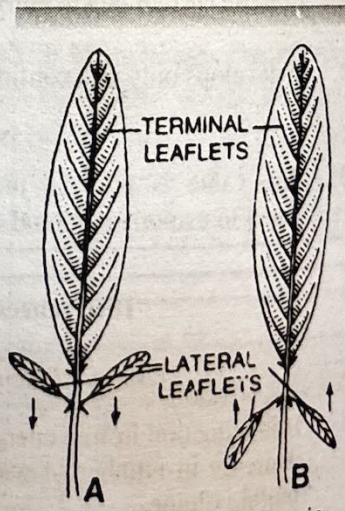


Fig. 11.12. Autonomic curvature movement of variation (turgor movement) in the two lateral leaflets of *Desmodium gyrans*.

(vi) The opening and closing of stomata are caused by gain and loss of turgidity by their guard cells. They are hence often called "turgor operated valves."

(vii) Turgor pressure (pressure potential or hydrostatic pressure) keeps a check on the excessive entry of water into cells.

(viii) Autochory of some fruits is dependent upon release of turgor pressure.

Osmotic Relations of Plant Cells (Fig. 11.13)

A plant cell functions as an osmotic apparatus or osmotic system. It is bathed in a water

medium or lies in contact with other cells having water. A typical plant cell has a permeable elastic wall, a semipermeable membrane (plasmalemma or plasma membrane alone or alongwith cytoplasm and tonoplast) and an osmotically active solution called **cell sap** (contained in the central vacuole). The osmotically active cell sap has an osmotic potential (ψ_s or OP). It causes the osmotic entry of water which develops a turgor pressure (TP) or pressure potential (ψ_p). The osmotic status of the cell is written as, $\psi_w = \psi_s + \psi_p$ or DPD = OP – TP (= WP). ψ_s or solute potential is a negative force. It causes entry of water into the cell. As a result a cell protoplast swells and develops the positive force of ψ_p. ψ_p is kept under check by **wall pressure**. The cell where wall is absent cannot counteract pressure potential. It will continue to absorb water due to ψ_s till it bursts. It is because of this fact that the animal cells are not bathed in water but instead are surrounded by nearly isotonic tissue fluid.

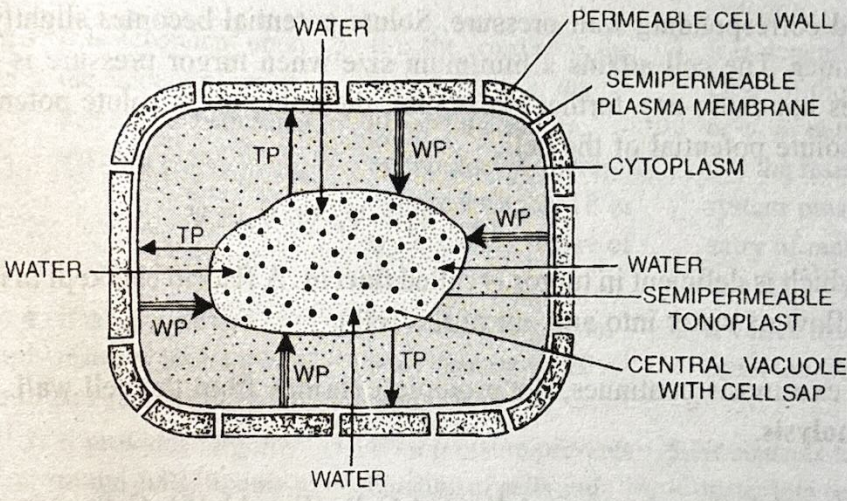


Fig. 11.13. Plant cell as an osmotic system.

Being a positive force, ψ_p opposes the entry of water into the cell.

(a) **Rise in Turgidity**. A flaccid cell placed in hypotonic solution will absorb water. The cell

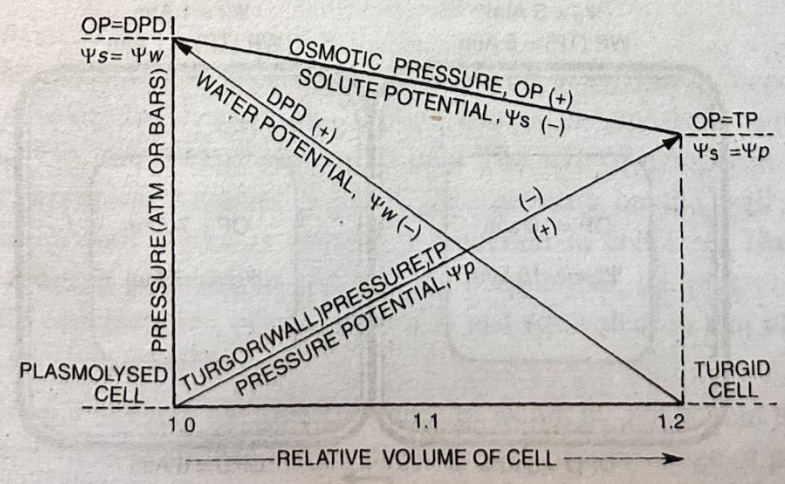


Fig. 11.14. Relationship between OP (= ψ_s), TP (= WP or ψ_p) and DPD (= ψ_w) of a cell. Note that DPD ($-\psi_w$) is zero when TP (ψ_p) becomes equivalent to OP (= ψ_s) while DPD (= ψ_w) becomes equal to OP (ψ_s) when TP (= ψ_p) is nil as in a plasmolysed cell.

swells up. The value of turgor pressure rises while that of solute potential becomes slightly less negative. As the cell becomes fully turgid, the value of turgor pressure becomes equal to that of solute potential (ψ_s) so that water potential (ψ_w) or DPD becomes either zero or equal to that of external hypotonic solution.

$$\psi_w = \psi_s + \psi_p = 0$$

Though there is no net movement of water between the cell and its environment, equilibrium is dynamic and not static. Equal exchange of water molecules continues between the cell and its environment.

(b) **Loss of Turgidity**. If plant cell happens to be bathed in hypertonic solution, it loses water through the process of exosmosis. The loss of water is first from cytoplasm and then central vacuole. As a result, the protoplast is reduced in size. This decreases turgor pressure or pressure potential and corresponding wall pressure. Solute potential becomes slightly more negative due to loss of water. The cell attains a minimum size when turgor pressure is zero. If the external solution does not cause any further exosmosis, the value of its solute potential will be equal or isotonic to solute potential of the cell.

$$\psi_w = \psi_s + \psi_p \text{ or } \psi_w = \psi_s$$

A cell which is deficient in turgor is called **flaccid**. A flaccid cell kept in isotonic solution will show equal flow of water into and out of the cell.

In case exosmosis continues, the protoplast shrinks from the cell wall. The phenomenon is called **plasmolysis**.

(c) **Water Relations between Adjacent Cells** (Fig. 11.15). Cells gain or lose water among themselves on the basis of their water potential (or DPD) and not their solute or osmotic potentials. A cell having more negative osmotic potential and high turgor pressure can lose water to a cell having less negative osmotic potential provided it has still lower turgor pressure.

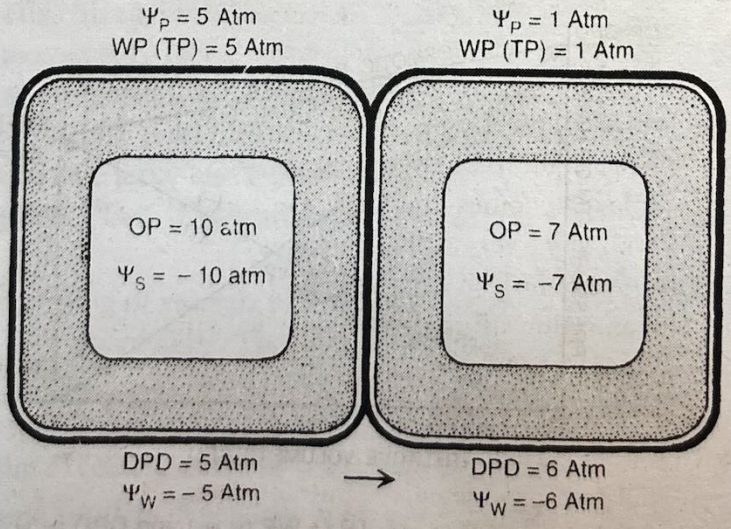


Fig. 11.15. Development of higher DPD (lower ψ_w) in a cell having lower OP (comparatively higher ψ_s) due to reduced TP (ψ_p) or WP.

Differences amongst OP (Ψs), TP (Ψp), WP and DPD (Ψw)

OP = ψ_s	*TP = ψ_p*	*WP*	*DPD = Ψ_w*
1. It is potential pressure that can develop in a solution when it is separated from pure solvent by a semipermeable membrane.	1. It is hydrostatic pressure which develops in a system due to osmotic entry of solvent in it.	1. It is the force exerted by the wall against expansion of osmotic system.	1. It is reduction in diffusion pressure or free energy of a solvent in an osmotic system over pure solvent.
2. It can develop in both confined and unconfined systems.	2. It develops only in a confined system.	2. Wall pressure occurs in a confined system.	2. It is found both in confined and unconfined systems.
3. It is dependent upon the number of solute particles in the solution.	3. It is dependent upon the amount of water that enters a confined system.	3. It is the resistance, the wall holds over the expanding osmotic system and is, therefore, dependent upon TP or ψ_p as well as nature of wall.	3. It is dependent upon OP or ψ_s of the system, OP or ψ_s of outside solution and the resistance that system puts against entry of more solvent into it.
4. OP or Ψ_s changes slightly in an osmotic system.	4. It is variable and changes from zero to equal the OP.	4. It is commonly equal and opposite to TP or ψ_p.	4. It varies from zero to equal the OP or ψ_s.
5. It helps in retaining water inside cells.	5. It provides turgidity to the cells, tissues and softer organs.	5. Wall pressure prevents bursting of cells and limits expansion.	5. It controls entry of water into cells and water relations amongst cells.
6. OP or ψs causes movement of water across a semipermeable membrane.	6. Development of turgor pressure or pressure potential is essential for growth of cells.	6. Reduction of wall pressure is required for growth of cells.	6. DPD or ψ_w determines whether a cell will lose or gain water from an external solution or adjacent cells.

PLASMOLYSIS

Shrinkage of the protoplast of a cell from its cell wall under the influence of a hypertonic solution is called plasmolysis. Hypertonic solution causes **exosmosis** or withdrawal of water from cytoplasm and then the central vacuole of cell. The size of cytoplasm as well as central vacuole and hence protoplast becomes reduced. The pressure on the wall is simultaneously reduced and the elastic wall contracts causing a reduction in cell size. This is first stage of plasmolysis called **limiting plasmolysis**. At limiting plasmolysis, the pressure potential (ψ_p) is zero and the osmotic concentration of cell interior is just equivalent to that of external solution (isotonic). The cell is called **flaccid**.

The extra hypertonic external solution continues to withdraw water from the central vacuole by exosmosis. Central vacuole shrinks further causing a similar shrinkage of protoplast from the cell wall. Pressure potential becomes negative. Initially the protoplast withdraws itself from the corners. This stage is known as **incipient plasmolysis**. The hypertonic solution now enters the cell in between the protoplast and the cell wall. Due to continued exosmosis, protoplast shrinks further and withdraws from the cell wall except one or a few points. It is known as **evident plasmolysis**.

Deplasmolysis

The swelling up of a plasmolysed protoplast under the influence of hypotonic solution or water is called deplasmolysis. It is due to **endosmosis**. Deplasmolysis is possible only immediately after plasmolysis otherwise the cell protoplast becomes permanently damaged. During deplasmolysis water diffuses into protoplast. It enters the central vacuole and cytoplasm. Consequently, the protoplast swells up. It first comes in contact with cell wall and then starts building a pressure on cell wall. This pressure is called turgor pressure. It makes the cell turgid.

Differences between Plasmolysis and Deplasmolysis

Plasmolysis	*Deplasmolysis*
1. It occurs when a tissue is placed in hypertonic solution.	1. Deplasmolysis occurs when freshly plasmolysed cells are kept in hypotonic solution or pure solvent.
2. Plasmolysis involves shrinkage of protoplast from the cell wall.	2. It is swelling of shrunken protoplast so as to come in contact with cell wall.
3. Plasmolysis is a result of exosmosis.	3. Deplasmolysis is a result of endosmosis.
4. Prolonged plasmolysis is not reversible.	4. Deplasmolysis is reversible even after an interval.

Expt. 4. Experiment to show Plasmolysis

Apparatus. A fresh filament of *Spirogyra* or a fresh peel from the lower leaf surface of *Rhoeo spathacea* (= *R. discolor* = *Tradescantia discolor*), 10% solution of potassium nitrate or common salt, a slide, cover slip, microscope, water, dropper and a piece of blotting paper.

Working. Mount a fresh filament of *Spirogyra* or peel of lower leaf surface of *Rheo spathacea* (= *R. discolor*) on a slide in a drop of water. Examine it under microscope and note that the cells are fully distended or turgid. Now replace the drop of water with a drop of 10% solution of potassium nitrate or common salt. The cells shrink in size. The shrinking protoplast becomes conspicuous due to presence of ribbon-shaped chloroplasts in *Spirogyra* and coloured sap in *Rhoeo*. It is followed by the separation of the protoplast from the cell wall due to its contraction. This shrinkage of the protoplast from the cell wall under the influence of a strong solution is called plasmolysis (Figs. 11.16 – 17).

If potassium nitrate or common salt solution is now replaced by water again, the protoplast starts swelling. It comes in contact with the cell wall and the cell regains its original size. The swelling up of the plasmolysed protoplast under the influence of a weak solution or water is called **deplasmolysis** (Fig. 11.16D).

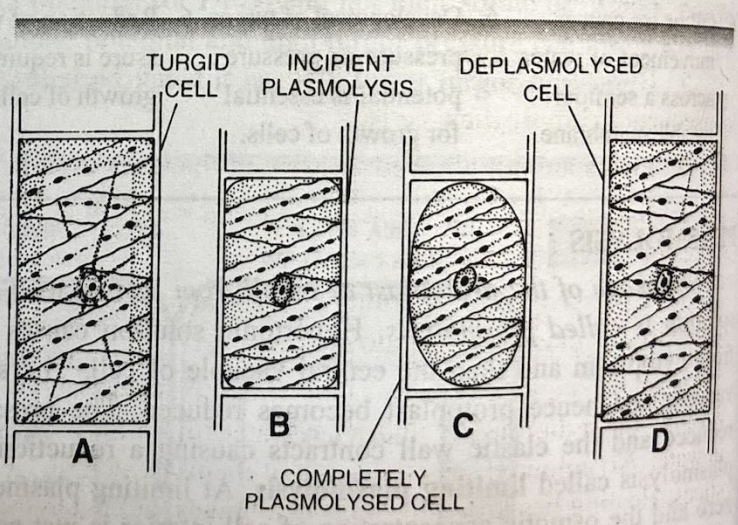


Fig. 11.16. Plasmolysis in *Spirogyra* cells. A, turgid cell; B, incipiently plasmolysed cell; C, plasmolysed cell; D, deplasmolysed cell.

Results. (i) The shrinkage of the protoplast under the influence of 10% potassium nitrate or common salt solution and later its swelling when placed in water shows that the protoplast possesses an osmotically active solution in its interior. The solution is called **cell sap**. (ii) The cell wall is fully permeable. (iii) The contraction of the cell as a whole is due to the reduction in the turgor pressure till the wall pressure becomes zero. When the wall pressure becomes zero, the cell does not contract further. Only the protoplast shrinks

now. (iv) Shrinkage of protoplast during plasmolysis and its expansion during deplasmolysis points out that the cytoplasm lying around the central vacuole acts as a semi-permeable membrane. (v) 10% potassium nitrate or common salt solution is stronger than cell sap.

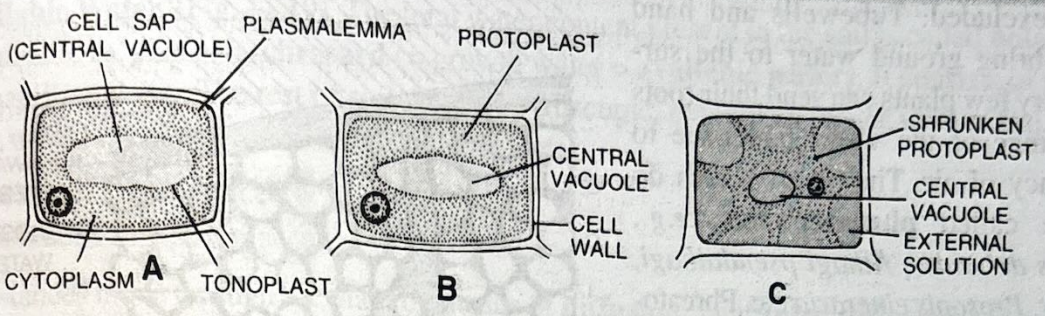


Fig. 11.17. Plasmolysis in a cell. A, turgid cell; B, incipient plasmolysis; C, evident plasmolysis.

Precautions. (i) The experimental material (*Spirogyra* filament, *Rhoeo* leaf peel) must be fresh and living. (ii) The external solution must not be too strong as to become toxic. (iii) Wash at least once the experimental material with external solution so that chances of dilution are minimised. (iv) For deplasmolysis, the material has to be washed at least twice with water.

Importance of Plasmolysis

1. Plasmolysis proves that the cell membrane is semipermeable.
2. It shows that the cell wall is elastic as well as permeable.
3. Osmotic pressure of a cell can be measured by plasmolysis. It will be roughly equivalent to the osmotic pressure of a solution which will be strong enough to cause only incipient plasmolysis.
4. Plasmolysis can be shown only by living cells. It can, therefore, determine whether a cell is living or dead.
5. By salting tennis lawns, the weeds can be killed due to permanent plasmolysis and consequent death of their cells.
6. Plants are not allowed to grow in the cracks of the walls by the method of salting.
7. Salting of pickles, meat and fish and sweetening of the jams and jellies with sugar, kill the spores of fungi and bacteria.
8. Excessive concentration of chemical fertilizers at one place in the soil should be avoided, otherwise the plants will die down.

Dead cells are fully permeable. It can be observed by cutting beet root into thin slices and washing them thoroughly under tap water till no more colour diffuses out. The slices are placed in water. No coloured sap comes out of them. Heat them. A reddish sap begins to come out of the slices. Heating has killed the cell membranes and made them permeable so that the sap diffuses out.

WATER ABSORPTION

SOIL WATER

Soil is the upper weathered, humus, mineral water and air containing layer of the earth's crust which supports plant life. Water is an important constituent of soil because all land plants depend upon it for their requirement of water. Deep in the soil and above the impermeable stratum, water occurs freely in the pervious rocky matter. It is called **ground water**. Ground water bearing

pervious stratum is known as **aquifer**. The upper layer of ground water is called **water table**. In the region of water table soil is completely saturated with water. Air is excluded. Tubewells and hand pumps bring ground water to the surface. Very few plants can send their roots upto fringe of the water table due to deficiency of air. The plants which do so, are called **phreatophytes**, *e.g.*, *Populus deltoides, Alhagi pseudalhagi, Tamarix, Prosopis cineraria* etc. Phreatophytes have been used successfully to locate under-ground water since the period of Varahmihira (Brihat Samhita, 5th century A.D.).

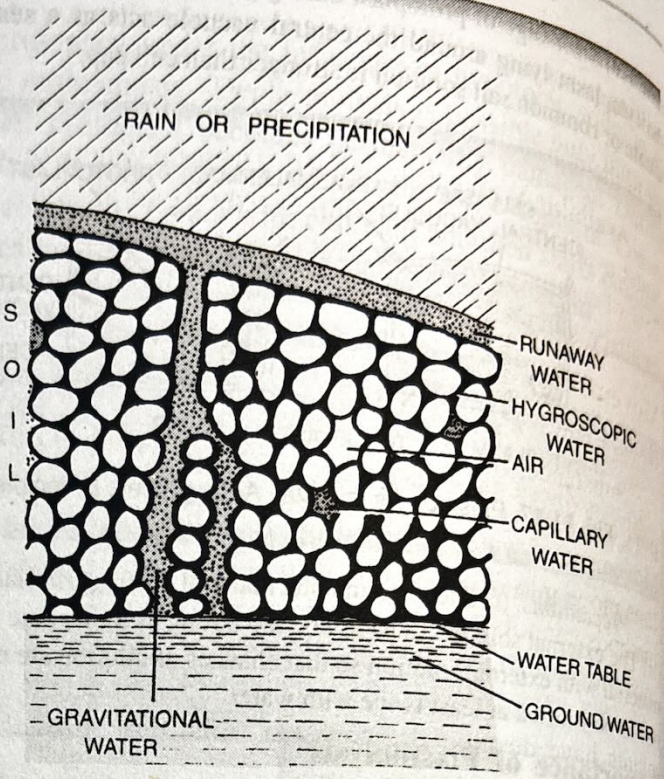


Fig. 11.18. Fate of water falling on soil in the form of rain.

Soil water, important to most plants, is the one present in 1–2m of soil because their roots are generally restricted to this region. Water is present in the soil in five forms— capillary water, gravitational water, hygroscopic water, combined water and water vapours. The ultimate source of all soil water is rain or irrigation. A part of rain water does not enter the soil but is drained away from soil-surface along the slope. It is called **run-away water** or **run-off** (Fig. 11.18).

Capillary Water. It is the water present in soil narrow spaces or **micropores** of soil having a diameter of 20 μm or below. The amount of capillary water which can be present in a soil depends upon the abundance of micropores. Capillary water is held in the soil by capillary forces. It, therefore, does not fall down to water table by gravity. Only capillary water is available to plant roots for absorption. However, roots are unable to absorb water from capillaries below the diameter of 0.2 μm.

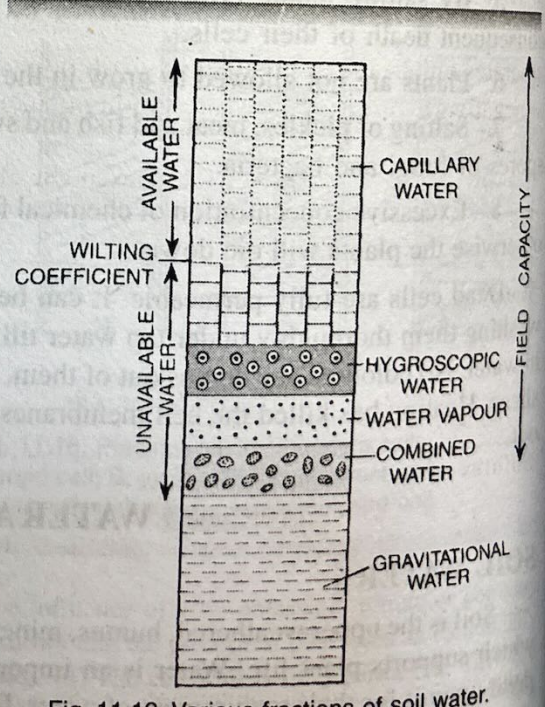


Fig. 11.19. Various fractions of soil water.

Excess rain or irrigation is not useful to plants. Rather it can be harmful because excess of water would expel soil air. This happens when flow of gravitational water is prevented and soil is covered with water for longer periods. The optimum or maximum amount of water retained per unit dry weight of soil after the stoppage of gravitational flow is called **field capacity**. It is 25–35% in common loam soils. Soil moisture beyond field capacity produces **water logging**. If soil water is not replenished from time to time, a stage is reached

when the plants growing in it become permanently wilted and die. It is known as **permanent wilting percentage** (PWP) or **permanent wilting coefficient** (PWC). At permanent wilting percentage the soil contains about 10% of water which is either present in extremely fine micropores or in the non-available stage.

Available Water (Fig. 11.19). The total water content present in the soil is called **holard**. The water available to plants is **chresard** (= growth water = **available water**). It consists of roughly 75% of capillary water. The rest of soil water (hygroscopic, combined, water vapour and 25% of capillary water) is called **echard** or unavailable water.

Movement of Substances (Long Distance Transport)

Substances move through the plant by means of **diffusion**, **facilitated diffusion**, **active transport** and **mass** or **bulk flow**. Gases move into and out of the plant entirely through diffusion. Movement of water into and out of cells occurs by a special type of diffusion called osmosis. Ions move into cells through diffusion, facilitated diffusion and active transport. However, these methods cannot provide a mechanism for translocation or long distance transport. For example, movement of a molecule through diffusion across a cell of 50 μm size will require 2.5 seconds. 1 metre transport through diffusion will approximately take 32 years. To overcome this deficiency, plants have developed a **mass** or **bulk flow system** which operates through development of pressure difference between the source and sink. In mass or bulk flow all the susbtances dissolved or suspended in solution travel at the same pace, just as silt suspended in the flowing river. It is quite different from diffusion where substances move independently according to their concentration gradients.

Long distance bulk movement of substances that occurs through conducting or vascular tissues of plants is called translocation. There are two vascular tissues, xylem and phloem. Xylem **translocation** is mainly from roots to aerial parts. It passes water with mineral salts, some organic nitrogen and hormones. Phloem translocates organic substances and inorganic solutes first from leaves to all other parts of the plant and storage organs. Storage organs re-export organic nutrients to those parts which require the same as newly formed leaves and fruits. Translocation operates either due to positive hydrostatic pressure gradient (like a garden hose) as in phloem or a negative hydrostatic pressure gradient (like suction through a straw) as in xylem.

Table 11.2. Movement of Substances through the Plant

	Uptake	Transport	Elimination
Water	osmosis into root	mass flow through xylem	diffusion (transpiration) through stomata (also small loss from cuticle and lenticels)
Solutes	diffusion or active transport into root	mass flow through xylem (mainly inorganic solutes) or phloem (mainly organic solutes)	shedding of leaves, bark, fruits and seeds; otherwise retained until death or passed to next generation in embryo of seed
Gases	diffusion through stomata, lenticels,	diffusion through intercellular spaces	diffusion through stomata, lenticels, epidermis

WATER ABSORBING SYSTEM

Plants have the potentiality to absorb water through their entire surface right from root, stem, leaves, flowers, etc. However, as water is available mostly in the soil, only the underground root system is specialized to absorb water. Roots are often extensive and grow rapidly in the soil. Ditmer (1937) has found the total length of the root system of a 4-month old Rye plant (*Secale cereale*) to be 620 km with a daily increase of 5 km. The surface area was calculated to be 255 square metres. Root ends of Maize grow by 6% of their volume every ten minutes (Hsiao, 1973). Such a spreading and growing root system allows the plant to absorb water efficiently from a restricted area in which it occurs.

In roots, the most efficient region of water absorption is the root hair zone. Each root hair zone has thousands of root hairs. Ditmer has estimated that a four month old Rye plant bears as many as 14 billion root hairs, with a length of over 10,000 km and total surface area of over 400 square metres. Root hairs are specialized for water absorption. They are tubular outgrowths of 50–1500 μm (0.05–1.5 mm) length and 10 μm in breadth. Each root hair has a central vacuole filled with osmotically active cell sap and a peripheral cytoplasm. The wall is thin and permeable with pectic substances in the outer layer and cellulose on the inner layer. Root hairs pass into capillary micropores, get cemented to soil particles by pectic compounds and absorb capillary water.

Pathways of Water Movements in Roots

There are two pathways of water passage from root hairs to xylem inside the root, apoplast and symplast (Figs. 11.20–21). (i) **Apoplast Pathway.** Here water passes from root hair to xylem through the walls of intervening cells without crossing any membrane or cytoplasm. The pathway provides the least resistance to movement of water. However, it is interrupted by the presence of impermeable lignosuberin **casparian strips** in the walls of endodermal cells. (ii) **Symplast Pathway.** Water passes from cell to cell through their protoplasm. It does not enter cell vacuoles. The cytoplasm of the adjacent cells are connected through bridges called **plasmodesmata**. For entering into symplast, water has to pass through plasmalemma (cell membrane) atleast at one place. It is also called **transmembrane pathway**.

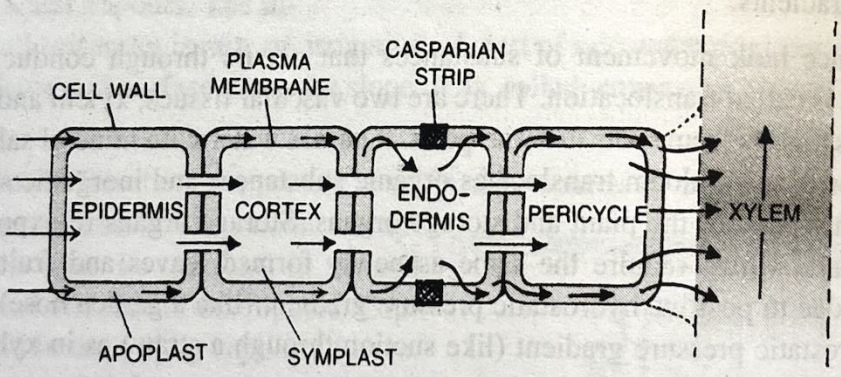


Fig. 11.20. Pathways of water movement inside the root.

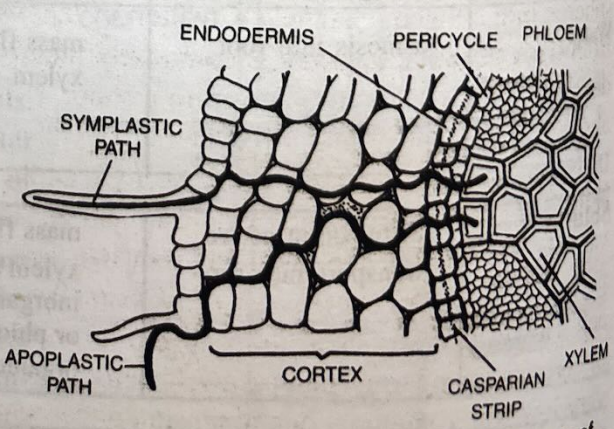


Fig. 11.21. Apoplastic and symplastic pathways of water and ions transport across the root.

Symplastic movement is aided by **cytoplasmic streaming** of individual cells. It is, however, slower than apoplastic movements.

Both the pathways are involved in the movement across the root. Water flows via apoplast in the cortex. It enters the symplast pathway in the endodermis where walls are impervious to flow of water due to the presence of casparian strips. Here, only plasmodesmata are helpful to allow passage of water into pericycle from where it enters the xylem. Mineral nutrients also have the same pathway as that of water. However, their absorption and passage into symplast mostly occurs through active absorption. Once inside the xylem, the movement is purely along the pressure gradient.

Mycorrhizal Water Absorption. In mycorrhiza a large number of fungal hyphae are associated with the young roots. The fungal hyphae extend to sufficient distance into the soil. They have a large surface area. The hyphae are specialised to absorb both water and minerals. The two are handed over to the root which provides the fungus with both sugars and N-containing compounds. Mycorrhizal association between fungus and root is often obligate. *Pinus* and orchid seeds do not germinate and establish themselves into plants without mycorrhizal association.

Differences between Apoplast and Symplast Pathways of Water Movement

Apoplast Pathway	*Symplast Pathway*
1. It consists of nonliving parts of plant body, *i.e.*, cell walls and intercellular spaces.	1. It consists of living parts of plant body, *i.e.*, protoplasts connected by plasmodesmata.
2. There is little resistance in the movement of water.	2. Some resistance occurs in the movement of water through symplast.
3. It is faster.	3. It is slightly slower.
4. Metabolic state of root does not affect apoplast pathway.	4. Metabolic state of root directly affects symplast pathway.

MECHANISM OF WATER ABSORPTION

Water absorption is of two types, passive and active (Renner, 1912, 1915).

Passive Water Absorption

The force for this type of water absorption originates in the aerial parts of the plant due to loss of water in transpiration. This creates a tension or low water potential of several atmospheres in the xylem channels. Creation of tension in the xylem channels of the plant is evident from (i) A negative pressure is commonly found in the xylem sap. It is because of it that water does not spill out if a cut is given to a shoot. (ii) Water can be absorbed by a shoot even in the absence of the root system. (iii) The rate of water absorption is approximately equal to the rate of transpiration. Root hairs function as tiny osmotic systems. Each root hair has a thin permeable cell wall, a semi-permeable cytoplasm and an osmotically active cell sap present in the central vacuole. Because of the latter a root hair cell has a water potential of –3 to –8 bars. Water potential of the soil water is –.1 to –.3 bars. As a result water of the soil passes into the root hair cell. However, water does not pass into its vacuole. Instead it passes into apoplast and symplast of cortical, endodermal and pericycle cells and enter the xylem channels passively because of the very low water potential due to tension under which water is present in them, caused by transpiration in the aerial parts. A gradient of water potential exists between root hair cell, cortical cell, endodermal, pericycle and xylem channels so that flow of water is not interrupted.

Active Water Absorption

It is the absorption of water due to forces present in the root. Living cells in active metabolic condition are essential for this. Auxins are known to enhance water absorption (even from hypertonic solution) while respiratory inhibitors reduce the same. Therefore, energy (from respiration) is involved in active water absorption. Water absorption from soil and its inward movement may occur due to osmosis. Passage of water from living cells to the xylem channels can occur by : (i) Accumulation of sugars or salts in the tracheary elements of xylem due to either secretion by the nearby living cells or left there during decay of their protoplasts. (ii) Development of **bioelectric potential** favourable for movement of water into xylary channels. (iii) Active pumping of water by the surrounding living cells into tracheary elements.

Root pressure is a manifestation of active water absorption.

Differences between Active and Passive Water Absorption

Active Water Absorption	*Passive Water Absorption*
1. It cannot occur in the absence of roots.	1. Passive water absorption can occur even in the absence of roots.
2. Root cells play an active role in this type of water absorption.	2. Root cells have no active role in this type of water absorption.
3. Living root cells either pump water into xylem or deposit solutes in the same.	3. Transpiration creates a tension in xylem.
4. Force for active water absorption lies in the roots.	4. Force for this type of water absorption develops in the shoot.
5. It is found in certain seasons only.	5. It is found throughout the year.
6. Active water absorption is reported in some plants only.	6. Passive water absorption occurs in all plants.
7. It uses metabolic energy.	7. It uses radiation energy.
8. Active water absorption is immediately influenced by metabolic poisons.	8. Metabolic poisons do not have any immediate effect on passive water absorption.
9. It is not influenced by transpiration.	9. It is dependent upon transpiration.
10. It creates a positive pressure in the xylem channels.	10. Passive water absorption produces a negative pressure in xylem channels.
11. It is manifested in the form of root pressure.	11. It is manifested in the form of transpiration pull.

ASCENT OF SAP

(Translocation of Water)

Sap is water with dissolved ingredients (minerals). The upward movement of water from roots towards the tips of stem branches and their leaves is called ascent of sap. It occurs through the tracheary elements of xylem. That the ascent of sap occurs through xylem can be demonstrated by the following experiment.

Experiment 5. Stain Test

Apparatus. A leafy shoot (*e.g.*, Balsam) preferably with white flowers freshly cut under water, 2% eosine solution, a stand, razor, slide and microscope.

Working. Take a leafy shoot freshly cut under water. Dip the cut end of the shoot in an eosine solution contained in a beaker. Hold the leafy shoot erect by means of a stand.

After some time veins of the leaves will become red (Fig. 11.22 A). Flowers develop the same colour. Even stem may look reddish. Cut thin transverse sections of the stem and leaves. Observe them under the microscope. The walls of tracheids and vessels will be found coloured (Fig. 11.22 B).

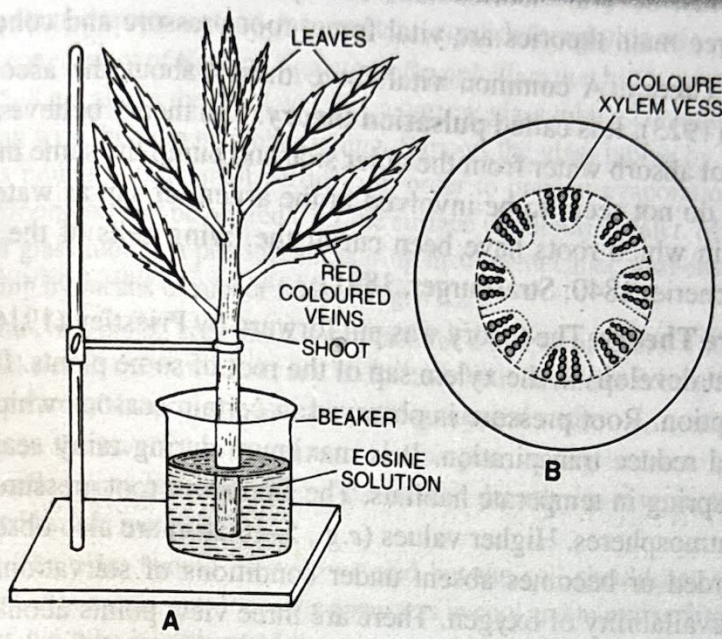


Fig. 11.22. Eosine test to demonstrate ascent of sap.

Results. The veins of the leaf consist of vascular bundles. The appearance of red colour in the vein of leaf shows that the coloured water travels through the vascular bundles. The microscopic examination of the sections proves that the coloured water moves through vessels and tracheids of xylem.

Expt. 6. Ringing Experiment (Fig. 11.23)

Apparatus. Two leafy shoots cut under water, a fine knife, a needle, two beakers, stand, water.

Working. Cut two leafy shoots under water. Keep their lower ends dipping in water. In one shoot remove 2–4 cm long ring of bark roughly in the middle region of the shoot. Remove the pith of the stem of this or basal 4–6 cm long region by means of a needle. Remove the xylem in the middle of the second shoot. Fix the shoots to stand and allow the apparatus as such for 1–2 days. The leaves of the first shoot will remain turgid while those of the second shoot would get wilted.

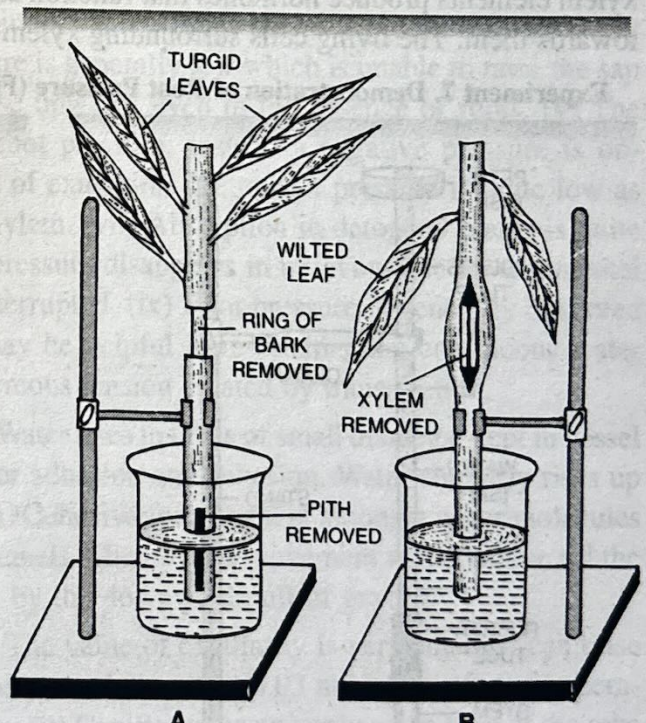


Fig. 11.23. Determination of path of ascent of sap. A, shoot with bark and pith removed remains turgid. B, shoot with xylem removed shows wilting of leaves.

Results. In the first shoot the leaves remain turgid even after 24 hours showing clearly that water continues to rise upwards the leafy shoot despite removal of bark and pith. Removal of bark breaks the continuity of epidermis, cortex, and phloem. As pith has also been discontinued, it shows clearly that epidermis, cortex, phloem and pith do not take part in transport of sap or water. The only tissue left intact is xylem. Xylem, therefore, must be the tissue taking part in the transport of water. This is confirmed from the wilting of the second shoot in which xylem has been discontinued.

Theories of Ascent of Sap. Water or sap is lifted from near the root tip to the shoot tip against the force of gravity, sometimes to height of 100 metres. The rate of translocation is 25–75

cm/minute (15–45 m/hr). Several theories have been put forward to explain the mechanism of ascent of sap. The three main theories are vital force, root pressure and cohesion tension.

1. **Vital Force Theory**. A common vital force theory about the ascent of sap was put forward by J.C. Bose (1923). It is called **pulsation theory**. The theory believes that the innermost cortical cells of the root absorb water from the outer side and pump the same into xylem channels. However, living cells do not seem to be involved in the ascent of sap as water continues to rise upward in the plant in which roots have been cut or the living cells of the stem are killed by poison and heat (Boucherie, 1840; Strasburger, 1891).

2. **Root Pressure Theory**. The theory was put forward by Priestley (1916). Root pressure is a positive pressure that develops in the xylem sap of the root of some plants. It is a manifestation of active water absorption. Root pressure is observed in certain seasons which favour optimum metabolic activity and reduce transpiration. It is maximum during rainy season in the tropical countries and during spring in temperate habitats. The amount of root pressure commonly met in plants is 1–2 bars or atmospheres. Higher values (*e.g.*, 5–10 atm) are also observed occasionally. Root pressure is retarded or becomes absent under conditions of starvation, low temperature, drought and reduced availability of oxygen. There are three view points about the mechanism of root pressure development: (a) **Osmotic**. Tracheary elements of xylem accumulate salts and sugars. High solute concentration causes withdrawal of water from the surrounding cells as well as from the normal pathway of water absorption. As a result a positive pressure develops in the sap of xylem. (ii) **Electro-osmotic**. A bioelectric potential exists between the xylem channels and surrounding cells which favour the passage of water into them. (iii) **Nonosmotic**. Differentiating xylem elements produce hormones that function as metabolic sinks and cause movement of water towards them. The living cells surrounding xylem can actively pump water into them.

Experiment 7. Demonstration of Root Pressure (Figs. 11.24–25)

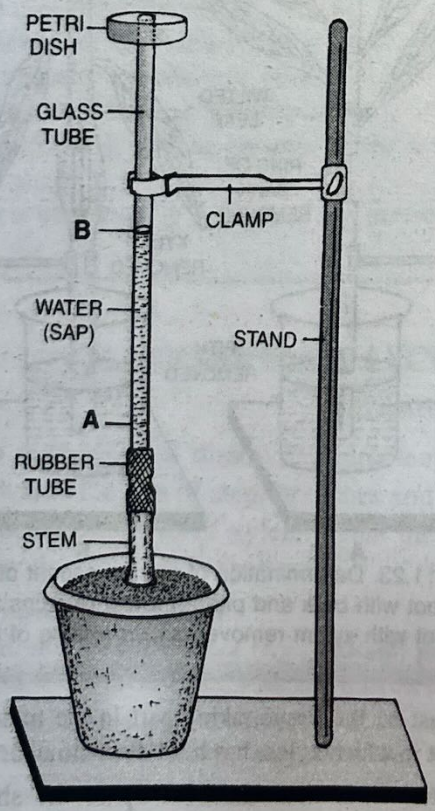


Fig. 11.24. Experiment to demonstrate root pressure.

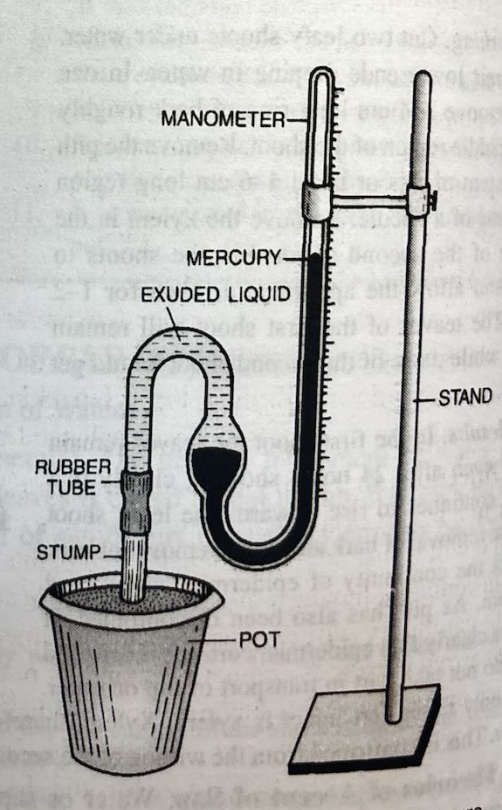


Fig. 11.25. Demonstration of root pressure.

Apparatus. A well watered potted plant of Balsam, Tomato or *Bryophyllum*, a knife, rubber tubing, a narrow glass tubing, coloured water, a stand, manometer, petridish (nondrying oil).

Working. Take a potted plant of Balsam, Tomato or *Bryophyllum* that has been well watered the previous day. Cut off its stem 5–8 cm above the soil level. Fix a narrow glass tubing containing some coloured water to the cut end of stump with the help of rubber tubing. Support the glass tubing by means of a stand. Cover the open end of glass tubing with a small petridish in order to prevent evaporation of water (Fig. 11.24). Instead a drop of nondrying oil can be poured over the surface of coloured water. Mark the level of coloured water as A. Instead of glass tubing, a pressure measuring instrument called **manometer** can also be fixed to the cut end of the stump by means of rubber tubing (Fig. 11.25).

Place the apparatus in a moist, cool and shady place for a couple of hours. The level of coloured water in the glass tubing will rise to the new mark, say B. In case the manometer is attached, the mercury level is found to be pushed upwards. The pressure is read on the graduated scale.

Results. The rise in the level of coloured water in the glass tubing is due to pumping of sap by root. The phenomenon is called **root pressure**. The same is read directly by manometer. A pressure of upto 5 atm. has been recorded by this method.

Precautions. (i) The plant should be well watered but the soil should not be flooded. (ii) The soil should not be deficient in minerals. (iii) Place the apparatus in cool and humid environment. (iv) Evaporation from the open end of the tube be prevented by using nondrying oil or petridish. (v) The plant should be vigorously growing.

Objections to Root Pressure Theory. (i) Root pressure has not been found in all plants. No or little root pressure has been seen in gymnosperms which have some of the tallest trees of the world. (ii) Root pressure is seen only during the most favourable periods of growth like spring or rainy season. At this time the xylem sap is strongly hypertonic to soil solution and transpiration rate is low. In summer when the water requirements are high, the root pressure is generally absent. (iii) The normally observed root pressure is generally low which is unable to raise the sap to the top of trees. (iv) Water continues to rise upwards even in the absence of roots. (v) The rapidly transpiring plants do not show any root pressure. Instead a negative pressure is observed in most of the plants. (vi) The amount of exudation due to root pressure is quite low as compared to the rate of passage through the xylem. (vii) Absorption in detopped plants is quite low as compared to intact plants. (viii) Root pressure disappears in unfavourable environmental conditions while ascent of sap continues uninterrupted. (ix) Root pressure is generally observed at night when evapotranspiration is low. It may be helpful in re-establishing continuous water chains in xylem which often break under enormous tension created by transpiration.

3. **Theory of Capillarity** (Bohm, 1863). Water rises in tubes of small diameter, kept in vessel having water, due to force of surface tension or adhesion and cohesion. Water similarly rises up in the walls of xylem channels due to adhesion. Cohesive force present amongst water molecules pulls the water upwards through the xylem channels. The upward movement will continue till the forces of adhesion and cohesion are balanced by the downward pull of gravity.

Objections to Theory of Capillarity. (i) The value of capillarity is very small. It can raise water to a height of about 1 metre in vessels of normal diameter (0.03 mm). Therefore, if operational it will be useful to only small sized palnts. (ii) Capillarity occurs only when base of the tube dips in container having water. Xylem vessels are not directly connected with soil water. (iii) Rise due to capillarity will increase when the lumen of vessels is less. Tall plants should, therefore, have narrow vessels as compared to smaller plants. The truth is, however, reverse. (iv) Capillarity cannot operate in plants having tracheids due to the presence of end walls.

4. **Cohesion Tension Theory** (Cohesion–Tension and Transpiration Pull Theory). The theory was put forward by Dixon and Joly in 1894. It was further improved by Dixon in 1914. Therefore, the theory is also named after him as **Dixon's theory of ascent of sap**. Today most of the workers believe in this theory. The main features of the theory are:

(a) *Continuous Water Column.* There is a continuous column of water from root through the stem and into the leaves. The water column is present in tracheary elements. The latter do operate separately but form a continuous system through their unthickened areas. Since there are a large number of tracheary elements running together, the blockage of one or a few of them does not cause any breakage in the continuity of water column (Scholander, 1957). The column of water does not fall down under the impact of gravity because forces of transpiration provide both energy and necessary pull. **Cohesion, adhesion** and **surface tension** keep the water in place.

(b) *Cohesion or Tensile Strength.* Water molecules remain attached to one another by a strong mutual force of attraction called **cohesion force**. The mutual attraction is due to **hydrogen bonds** formed amongst adjacent water molecules (Fig. 11.26). On account of cohesion force, the water column can bear a tension or pull of upto 100 atm (Mac Dougal, 1936). Therefore, the cohesion force is also called **tensile strength**. Its theoretical value is about 15000 atm but the measured value inside the tracheary elements ranges between 45 atm to 207 atm (Dixon and Joly, 1894). Water column does not further break its connection from the tracheary elements (vessels and tracheids) because of another force called **adhesion** force between their walls and water molecules. Water molecules are attracted to one another more than the water molecules in the gaseous state. It produces **surface tension** that accounts for high capillarity through tracheids and vessels.

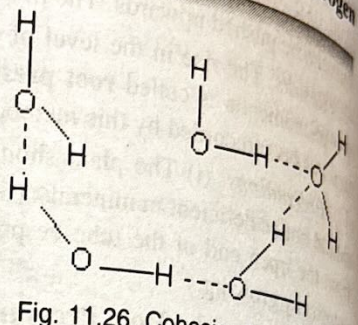


Fig. 11.26. Cohesion force due to hydrogen bonding between water molecules.

(c) *Development of Tension or Transpiration Pull.* Intercellular spaces present amongst mesophyll cells of the leaves are always saturated with water vapours. The latter come from the wet walls of mesophyll cells. The intercellular spaces of mesophyll are connected to the outside air through stomata. Outside air is seldom saturated with water vapours. It has a lower water potential than the moist air present inside the leaf. Therefore, water vapours diffuse out of the leaves. The mesophyll cells continue to lose water to the intercellular spaces. As a result curvature of meniscus holding water increases resulting in increase in surface tension and decrease in water potential, sometimes to –30 bars. The mesophyll cells withdraw water from the deeper cells as its molecules are held together by hydrogen bonds. The deeper cells in turn obtain water from

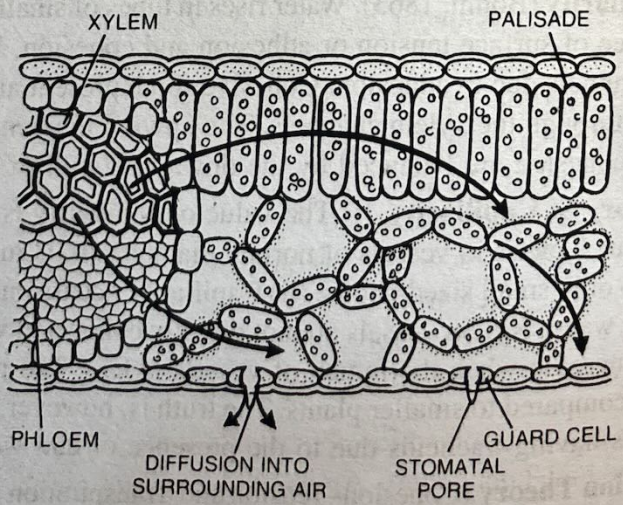


Fig. 11.27. Water movement in leaf and development of pressure gradient between outside air and leaf air spaces, leaf air spaces and mesophyll cells, mesophyll cells and water filled xylem of leaf veins.

the tracheary elements. The water in the tracheary elements would, therefore, come under **tension**. A similar tension is felt in millions of tracheary elements lying adjacent to the transpiring cells. It causes the whole water column of the plant to come under tension. As the tension develops due to transpiration, it is also called **transpiration pull**. On account of tension created by transpiration, the water column of the plant is pulled up passively from below to the top of the plant like a rope (Fig. 11.28). As a tension of one atmosphere is sufficient to pull water to a height of about 10 metres, a tension of 10–20 atm is sufficient to raise water to the height of the tallest tree over 130 m. It overcomes, (i) gravitational pull, (ii) resistance of narrow xylem channels and their end walls, (iii) resistance of living cells of the root that lie in the path of water from soil to xylem, (iv) resistance offered by water coming out of narrow capillary pores of the soil.

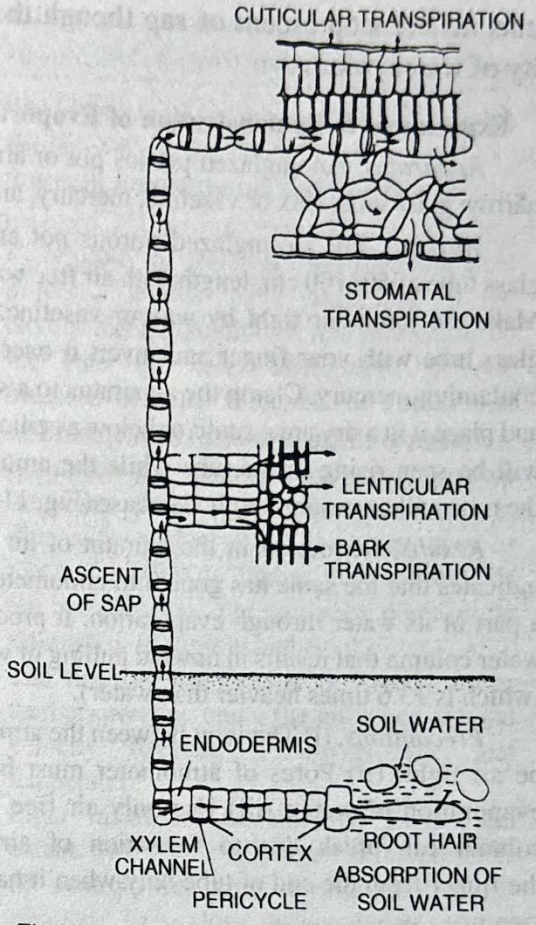


Fig. 11.28. Path of water through the plant.

Evidences. (i) The rate of water absorption and hence ascent of sap closely follows the rate of transpiration. (ii) Evaporation of water from a porous pot or atmometer can produce a tension in the water column present in attached tube. It can even raise a column of mercury to sufficient height (Fig. 11.29). (iii) Shoot attached to a tube having water and dipping in a beaker having mercury can cause the movement of mercury into the tube showing transpiration pull (Fig. 11.30). (iv) In a branch cut from a rapidly transpiring plant, water snaps away from the cut end showing that the water column is under tension. (v) With the help of dendrograph it is found that tree trunks contract during the day time and expand during the night. Contraction is caused by narrowing of tracheary elements when the contained water is under tension. (vi) The maximum tension observed in water column is 10–20 atm. It is sufficient to pull the water to the top of the tallest trees of even more than 130 metres in height. The tension cannot break the continuity of water column as cohesive force of xylem sap is 45 to 207 atm. (vii) Gymnosperms are at a disadvantage in the ascent of sap because of the presence of tracheids instead of vessels in angiosperms. However, tracheidal xylem is less prone to gravitation under tension. Therefore, most of the tall trees of the world are redwoods and conifers.

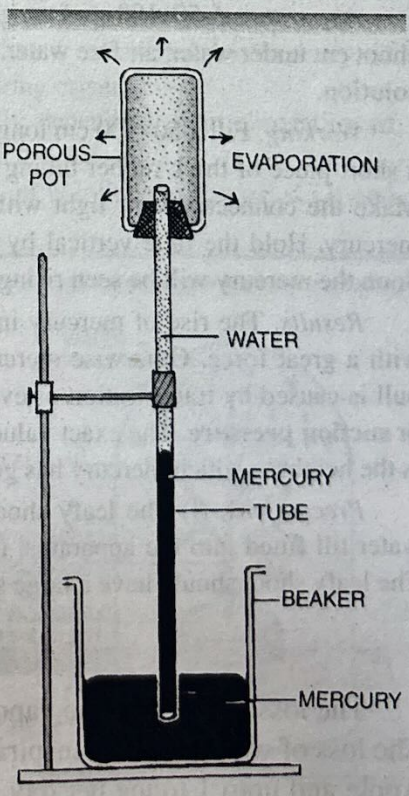


Fig. 11.29. Demonstration of pull due to evaporation.

Objections. (i) The gases dissolved in sap shall form air bubbles under tension and high temperature. Air bubbles would break the continuity of water column and stop ascent of sap due to transpiration pull. (ii) A tension of upto 100 atm has been reported in the xylem sap by Mac Dougal (1936) while the

cohesive force of sap can be as low as 45 atm. (iii) Overlapping cuts do not stop ascent of sap though they break the continuity of water column.

Experiment 8. Demonstration of Evaporation Pull.

Apparatus. An unglazed porous pot or atmometer, a cork, a long narrow glass tube, wax or vaseline, mercury, air free water.

Working. Fill an unglazed porous pot and a narrow but strong glass tube of 50–100 cm. length with air free water (boiled and cooled). Make the joints air tight by wax or vaseline. Cover the free end of glass tube with your finger and invert it over the base of the beaker containing mercury. Clamp the apparatus to a stand in upright position and place it in a dry area, sunlit or below a ceiling fan. Soon the mercury will be seen rising in the tube while the amount of water present in the tube will correspondingly decrease (Fig. 11.29).

Results. Reduction in the amount of air free water in the tube indicates that the same has gone into atmometer which must have lost a part of its water through evaporation. It produces the tension in the water column that results in upward pulling of water as well as mercury (which is 13.6 times heavier than water).

Precautions. (i) The joint between the atmometer and tube should be air tight. (ii) Pores of atmometer must be open to bring about evaporation of water. (iii) Use only air free water otherwise water column can break due to formation of air bubbles. (iv) Remove the finger from the end of tube only when it has thoroughly dipped in mercury.

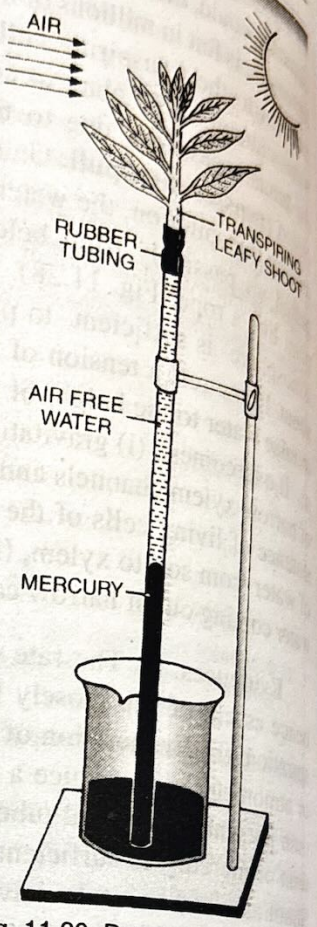


Fig. 11.30. Demonstration of pull due to transpiration.

Experiment 9. Demonstration of Transpiration Pull.

Apparatus. A 50–100 cm long glass tube, rubber tubing, fresh leafy shoot cut under water, air free water, mercury, beaker, stand and rubber solution.

Working. Fill a 50–100 cm long tube with air free water. Close one end of the tube with your finger. Fix a short piece of thick rubber tubing over the other end. Through it insert the cut end of a shoot in the tube. Make the connections air tight with rubber solution. Dip the free end of the tube in a beaker containing mercury. Hold the tube vertical by means of a stand (Fig. 11.30). Place the apparatus in open dry place. Soon the mercury will be seen rising upwards in the tube.

Results. The rise of mercury in the tube clearly shows that water in the tube is being pulled upwards with a great force. Otherwise mercury, which is 13.6 times heavier than water cannot rise upwards. This pull is caused by transpiration or evaporation of water from the shoot. Hence transpiration produces a **pull** or **suction pressure**. The exact value of the pull is calculated by $\pi r^2 h \times 13.6$ where r is radius of the tube, h is the height to which mercury has gone up.

Precautions. (i) The leafy shoot should be cut under water. Its lower end should be kept dipping in water till fitted into the apparatus. (ii) The joint must be completely air tight. (iii) Use air free water. (iv) The leafy shoot should have a large surface area with good rate of transpiration.

TRANSPIRATION

The loss of water in the vapour form from the exposed parts of a plant is called transpiration. The loss of water due to transpiration is quite high —2 litres per day in Sunflower, 36–45 litres in Apple and upto 1 tonne per day in Elm tree. Rather 98–99% of the water absorbed by a plant is lost in transpiration. Hardly 0.2% is used in photosynthesis while the remaining is retained in the plant during growth.

Differences between Evaporation and Transpiration

Evaporation	*Transpiration*
1. Water vapours are formed at the free surface of water.	1. Water vapours are formed mostly in internal tissues of the plant.
2. It takes place at the surface of non-living objects.	2. It occurs at the exposed surface of plants.
3. It is a physical process which is controlled by the environmental conditions like relative humidity and air current.	3. It is both a physical and physiological process. Besides being controlled by the environmental conditions, it is influenced by the rate of water absorption, osmotic pressure of cells, thickness of cuticle and number, position and opening of stomata.
4. Evaporation stops when the air is fully saturated.	4. Formation of vapours continues for some time even after the saturation of outside air. This is due to the fact that the temperature of the leaf is slightly higher than the outside air, and therefore, the saturation point of the internal air is slightly higher.
5. It varies directly according to the velocity of wind.	5. The rate of transpiration is slightly lower than evaporation under the influence of wind velocity because it lowers the leaf temperature.
6. Light does not directly influence the rate of evaporation.	6. Light influences transpiration to a great extent. Stomata usually open in the presence of sunlight resulting in full-scale transpiration. They close during darkness, thus lowering the rate of transpiration to a great extent.
7. Evaporation is comparatively faster.	7. It is a comparatively slow process.
8. It is not much influenced by the structure of the evaporating surface.	8. Transpiration is controlled by anatomy of the transpiring organ.
9. It continues as long as water is available on the surface.	9. It is largely dependent upon absorption of water from the soil.
10. CO_2, *p*H and hormones have no effect on evaporation.	10. Transpiration is influenced by *p*H, CO_2 and hormones.

Experiment 10. Demonstration of Transpiration

Apparatus. A well-watered potted plant, vaseline, oil cloth, strong thread or clamping rubber bands, glass slab and a bell jar.

Working. Take a small well watered potted plant. Cover the external surface of pot and its soil with oil cloth. Place the potted plant on a glass slab in a cooler place and invert a **dry bell jar** over it. Seal the edges of the bell jar with vaseline so that no air enters the apparatus from outside (Fig. 11.31). Leave the apparatus undisturbed. Soon the interior of the bell jar becomes misty. Afterwards drops of water will be found on the inner surface of the jar.

Results. The drops of water which appear on the inside of the bell jar cannot come from the outside air, nor from the water present in the soil of the pot because both have been properly sealed. The water vapours can come only from the exposed aerial shoot of the plant. Such a loss of water from the plant is called **transpiration**.

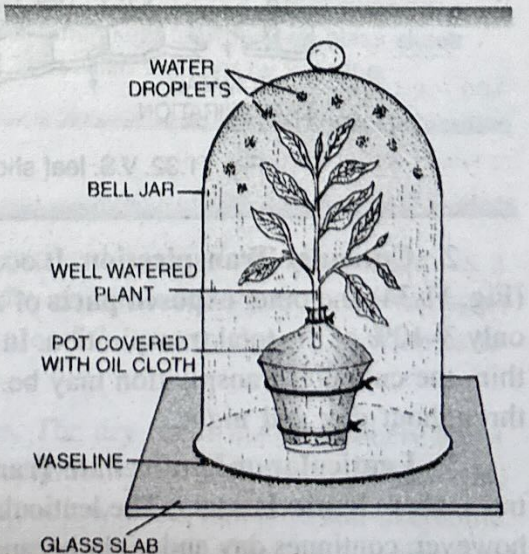


Fig. 11.31. Demonstration of transpiration by bell jar experiment.

Precautions. (i) Do not place apparatus in a very warm place as the water vapours will not be able to condense. (ii) Keep the apparatus undisturbed. (iii) Use a glass slab or smooth surface as the base for the apparatus. (iv) Seal the edges of bell jar so as to avoid the entry of water vapours from outside. (v) Cover the soil and the exterior of the pot properly with oil cloth.

Types of Transpiration

Most of the transpiration occurs through foliar surface or surface of the leaves. It is known as **foliar transpiration**. Foliar transpiration accounts for over 90% of the total transpiration. Young stems, flowers, fruits, etc. also transpire a lot. Mature stems transpire very little. Transpiration from stems is called **cauline transpiration**. Depending upon the plant surface transpiration is of the following four types— stomatal, cuticular, lenticular and bark.

1. **Stomatal Transpiration**. It is the most important type of transpiration. Stomatal transpiration constitutes about 50–97% of the total transpiration. It occurs through the **stomata**. The stomata are found mostly on the **leaves**. A few of them occur on the young stems, flowers and fruits. The stomata expose the wet interior of the plant to the atmosphere. The internal air, therefore, becomes saturated with water vapours. The outside air is seldom saturated with water except just after rains. **Water vapours**, therefore, pass **outwardly** through **stomata** by diffusion. More water evaporates from the internal cells to replace the outgoing water vapours (Fig. 11.32). The stomatal transpiration continues till the stomata are kept open.

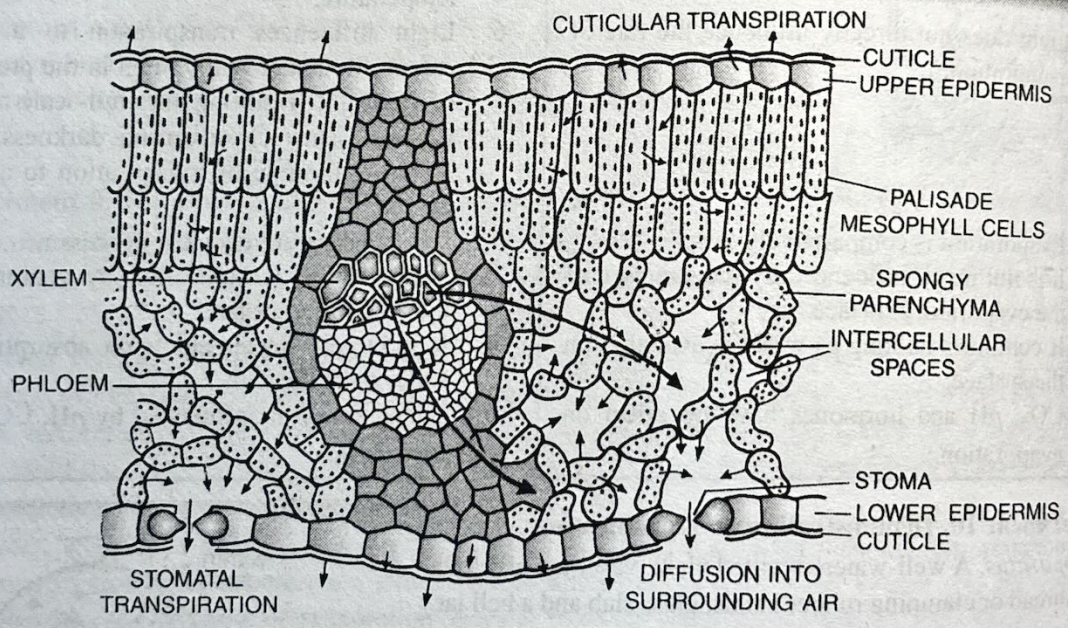


Fig. 11.32. V.S. leaf showing stomatal and cuticular transpiration.

2. **Cuticular Transpiration**. It occurs through the **cuticle** or **epidermal cells** of the **leaves** (Fig. 11.34) and other **exposed parts** of the plant. In common land plants cuticular transpiration is only 3–10% of the total transpiration. In herbaceous shade loving plants where the cuticle is very thin, the cuticular transpiration may be upto 50% of the total. Cuticular transpiration continues throughout day and night.

3. **Lenticular or Lenticellate Transpiration**. It is found only in the **woody branches** of the trees where **lenticels** occur. The lenticular transpiration is only 0.1% of the total transpiration. It, however, continues day and night because lenticels have no mechanism of closure. The **lenticels** connect the **atmospheric air** with the **cortical tissue** of the **stem** through the intercellular spaces present amongst the complementary cells.

4. **Bark Transpiration**. This type of transpiration occurs through corky covering of the stems. Bark transpiration is very little but its measured rate is often more than lenticular transpiration due to larger area. Like cuticular and lenticular types of transpiration, bark transpiration occurs continuously during day and night.

Expt. 11. Demonstration of Transpiration from Foliar Surface

Apparatus. 3–5% cobalt chloride solution, two small pieces of filter paper, desiccator or oven, forceps, leaf clasp, slides, vaseline, a potted plant or fresh shoot of Pipal or Mulberry with one end in water.

Working. Dip two small pieces of filter paper in 3–5% cobalt chloride solution. Take them out and dry in an oven or desiccator till they become **blue**.

Clean the lower surface of leaf gently with dry cotton. Place a dry cobalt chloride paper over it. Quickly cover the paper with a glass slide and seal its sides with vaseline. Fix them to the leaf clasp (Fig. 11.33). Within a few minutes the colour of the cobalt chloride paper will turn **pink**. No such change occurs in the dry cobalt chloride paper kept in between two glass slides with the edges sealed to prevent entry of water vapours from air (Fig. 11.34). Instead of glass slide and vaseline, cellotape can be used in both the cases.

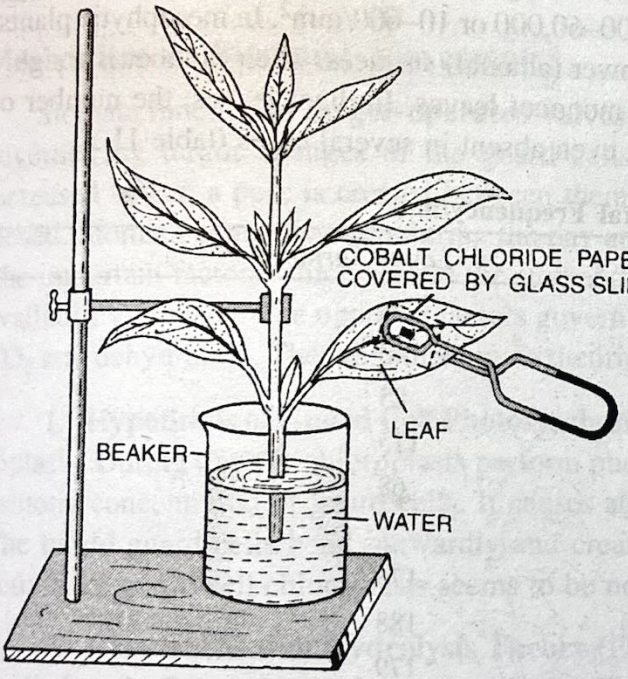


Fig. 11.33. Cobalt chloride paper test to demonstrate transpiration from foliar surface.

Results. Cobalt chloride is blue in the anhydrous condition but becomes pink in contact with water. The change of colour of the cobalt chloride paper from blue to pink clearly indicates that the paper has received water from the surface of leaf.

Precautions. (i) Use dry foreceps. (ii) Dry the leaf surface gently with dry cotton. (iii) Handle the leaf gently. (iv) Seal the edges of the slide completely but gently with vaseline.

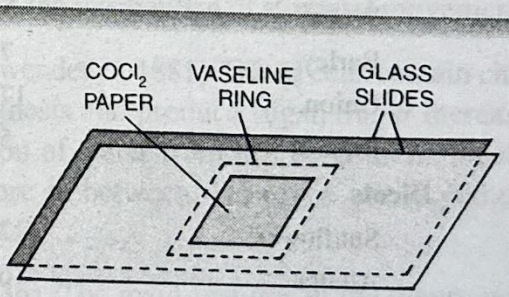


Fig. 11.34. Dry $CoCl_2$ paper remains blue when kept between two glass slides sealed together by vaseline.

Mechanism of Water Loss

In order to form vapours, water present inside the exposed parts of the plant requires a source of heat energy. It is the radiant energy during the day and heat energy from the transpiring organ during the night. In both the cases the temperature of the transpiring organs comes to lie 2–5°C below that of the atmosphere.

The atmosphere is rarely saturated with water vapours. The dry air of the atmosphere has a high DPD (or low water potential)–13.4 atm at 99% relative humidity or RH, 140 atm at 90% RH, 680 atm at 60% and 2055 atm at 20% RH. Such a high DPD or low water potential can overcome various types of resistances water molecules have to meet in changing from liquid phase to vapour phase and the movement of water vapours out of the transpiring organ. The intercellular spaces of the transpiring organ is almost saturated with water vapours. When the stomata are

open, the water vapours are drawn from the substomatal cavities to the outside air due to high DPD of the latter. This increases the DPD of the substomatal air which draws more water vapours from the intercellular spaces. The latter in turn get water vapours from the wet walls of mesophyll cells. Stomatal transpiration will continue till the stomata are open. Mechanism of lenticular transpiration is similar to that of stomatal transpiration.

Cuticle is not much permeable to water. However, its molecules absorb water from the epidermal cells by imbibition. The imbibed water is slowly lost to the atmosphere which has a high DPD. Imbibition flow is reduced by the thickness of cuticle. Therefore, a thick cuticle does not allow transpiration to occur through it. Cuticle is shrunken and thicker during the day but at night it expands and becomes loose. Therefore, cuticular transpiration can be more at night. Mechanism of bark transpiration is similar to that of cuticular transpiration.

Stomatal Apparatus (Fig. 11.35)

Stomata (= stomates) are tiny pore complexes found in the epidermis of leaves and other soft aerial parts. The size is 10–14 μm (range 7–38 μm) in length and 3–12 μm in breadth. The number of stomata per cm^2 of leaf surface varies from 1000–60,000 or 10–600/mm^2. In mesophytic plants, stomata occur both on the upper (adaxial) and lower (abaxial) surfaces. Their number is roughly equal on the two surfaces in grasses and other monocot leaves. In dicot leaves, the number of stomata on the upper surface is usually smaller, even absent in several cases (table 11.3).

Table 11.3. Stomatal Frequency/mm^2

	Upper Surface	*Lower Surface*
Monocots		
Wheat	50	40
Barley	70	85
Onion	175	175
Maize	52	68
Dicots		
Sunflower	120	175
Alfalfa	169	188
Geranium	20	179
Apple	0	387
Mulberry	0	480

Stomata are meant for the gaseous exchange but are also the main source of transpiration. Each stomate or stoma is surrounded by two small but specialized green epidermal cells called **guard cells**. Because of their small size, they are rapidly influenced by turgor changes. The guard cells are connected with the adjacent epidermal cells through plasmodesmata. They contain a few small chloroplasts with peripheral reticulum characteristic of chloroplasts showing C_4 photosynthesis. The guard cells also possess small vacuoles and microbodies. They store starch with the exception of a few. The walls are differentially thickened and elastic. They have folds for expansion (Srivastava and Singh, 1972). **Microfibrils** of these walls are oriented specifically to help in opening and closing of stomata.

In most of the plants the guard cells are **kidney shaped** in outline (Fig. 11.35 A-B). They are joined at their ends. The concavo-convex curvature of two guard cells is variable and causes stomatal pore to open and close. The walls of these guard cells are thickened on inner side. They have one or two pairs of wall extensions or **ledges** to prevent entry of water drops into stomata. The walls are thinner and more elastic on the outer side. When the stomata are to open, these

guard cells swell up on the outer side by the development of a high turgor pressure. The inner concave sides also bend out slightly so as to create a pore in between two guard cells. During closure movement, reverse changes occur.

In cereals, members of cyperaceae and some plams the guard cells are **dumb-bell shaped** in outline (Fig. 11.35 C-D). Their expanded ends are thin-walled while middle portions are highly thick-walled. In such cases opening and closing of the stomatal pore is caused by expansion and contraction of thin-walled ends of the guard cells.

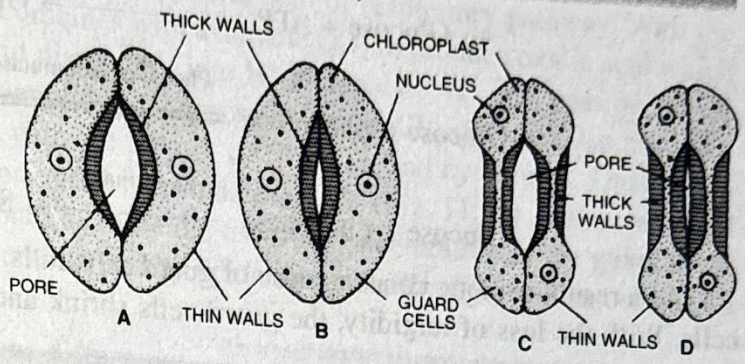


Fig. 11.35. Opened and closed stomata.
A, Dicotyledonous. B, Monocotyledonous.

Mechanism of Stomatal Movement

Stomata function as **turgor-operated valves** because their opening and closing movement is governed by turgor changes of the guard cells. Whenever, the guard cells swell up due to increased turgor, a pore is created between them. With the loss of turgor the stomatal pores are closed. Stomata generally open during the day and close during the night with a few exceptions. The important factors which govern the stomatal opening are light, high *p*H or reduced CO_2 and availability of water. The opposite factors govern stomatal closure, *viz.*, darkness, low *p*H or high CO_2 and dehydration. There are three main theories about the mechanism of stomatal movements:

1. **Hypothesis of Guard Cell Photosynthesis** (Schwendener, 1881). Guard cells contain chloroplasts. During day the chloroplasts perform photosynthesis and produce sugar. Sugar increases osmotic concentraton of guard cells. It causes absorption of water from nearby epidermal cells. The turgid guard cells bend outwardly and create a pore in between. However, photosynthetic activity of guard cell chloroplasts seems to be negligible.

2. **Classical Starch Hydrolysis Theory** (Fig. 11.36). The main features of the theory were spelled out by Sayre (1923). It was modified by Steward (1964). The guard cells contain starch. At low carbon dioxide concentration (in the morning achieved through photosynthesis by mesophyll and guard cells), *p*H of guard cells rises. It stimulates enzyme phosphorylase. Phosphorylase converts starch into glucose 1-phosphate. The latter is changed to glucose 6-phosphate which undergoes hydrolysis to produce glucose and phosphoric acid.

$$\text{Starch} + n\text{H}_3\text{PO}_4 \xrightarrow{\text{Phosphorylase}} n \text{ Glucose 1-phosphate}$$

$$\text{Glucose 1-phosphate} \underset{}{\overset{\text{Phosphoglucomutase}}{\rightleftharpoons}} \text{Glucose 6-phosphate}$$

$$\text{Glucose 6-phosphate} + \text{water} \xrightarrow{\text{Phosphatase}} \text{Glucose} + \text{H}_3\text{PO}_4$$

Glucose increases osmotic concentration of guard cells. On account of it, the guard cells absorb water from neighbouring cells, swell up and create a pore in between them. Evening closure of stomata is brought about by increased carbon dioxide content (due to stoppage of photosynthesis) of leaf. It decreases *p*H of guard cells and brings about phosphorylation of glucose. In the presence of phosphorylase, glucose 1-phosphate is changed into starch.

$$\text{Glucose + ATP} \xrightarrow{\text{Hexokinase}} \text{Glucose 6-phosphate + ADP}$$

$$\text{Glucose 6-phosphate} \underset{}{\overset{\text{Phosphoglucomutase}}{\rightleftharpoons}} \text{Glucose 1-phosphate}$$

$$\text{Glucose 1-phosphate} \xrightarrow{\text{Phosphatase}} \text{Starch + } H_3PO_4$$

As a result, osmotic concentration of guard cells falls. They lose water to adjacent epidermal cells. With the loss of turgidity, the guard cells shrink and close the pore in between them.

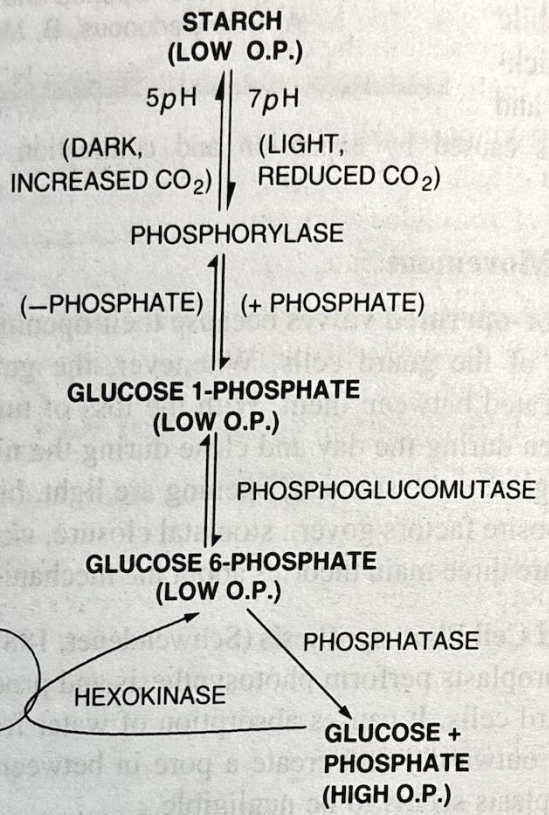


Fig. 11.36. Development of high and low osmotic pressures in guard cells through starch hydrolysis theory.

Objections. (i) Glucose is not found in guard cells at the time of stomatal opening. (ii) Starch $\rightleftharpoons$ Sugar changes are chemically slow while opening and closing of stomata are quite rapid. (iii) Wide changes in *p*H of guard cells cannot be explained on the basis of carbon dioxide concentration. (iv) Onion and some of its relatives do not possess starch or related polysaccharide that can be hydrolysed to the level of glucose. (v) Blue light has been found to be more effective than other wavelengths for opening of stomata. The same cannot be explained by starch hydrolysis theory. (vi) Hydrolysis of starch theory cannot account for high rise in osmotic pressure found in guard cells.

3. **Malate or K^+ ion Pump Hypothesis** (Modern Theory). The main features of the theory were put forward by Levitt (1974). According to this theory, *p*H of the guard cell can rise due to active H^+ uptake by guard cell chloroplasts or mitochondria, CO_2 assimilation by mesophyll and guard cells. A rise in *p*H causes hydrolysis of starch to form organic acids, especially phosphoenol pyruvate. Starch → Hexose Phosphate →Phosphoglyceric Acid →Phosphoenol Pyruvate.

Phosphoenol pyruvate can also be formed by pyruvic acid of respiratory pathway. With the help of PEP carboxylase (PEP case), it combines with available CO_2 to produce oxalic acid which gets changed into malic acid. Malic acid dissociates into H^+ and malate. H^+ ions pass out of the guard cells in exchange for K^+ ions. Some K^+ ions (accompanied by Cl^- ions) are also absorbed actively from adjacent epidermal cells with the help of cAMP, ATP and cytokinins. Guard cells maintain their electroneutrality by balancing K^+ with malate and Cl^- (Fig. 11.37). In the combined state they pass into the small vacuoles and increase the osmotic concentration of the guard cells. As a result guard cells absorb water from the nearby epidermal cells through endosmosis, swell up and create a pore in between them.

During stomatal closure, the H^+ ions diffuse out of the guard cell chloroplasts. It decreases *p*H of the guard cell cytoplasm. Any malate present in the cytoplasm combines with H^+ to form malic acid. Excess of malic acid inhibits its own biosynthesis. High CO_2 concentration also has a similar effect. Undissociated malic acid promotes leakage of ions (Jackson and Taylon, 1970). As a result K^+ ions dissociate from malate and pass out of the guard cells. Formation of abcisic acid (as during drought or midday) also promotes reversal of $H^+ \rightleftharpoons K^+$ pump and increases availability of H^+ inside the guard cell cytoplasm. Loss of K^+ ions decreases osmotic concentration of guard cells as compared to adjacent epidermal cells. This causes exosmosis and hence turgidity of the guard cells decreases. It closes the pore between the guard cells. Simultaneously the organic acids are metabolised to produce starch.

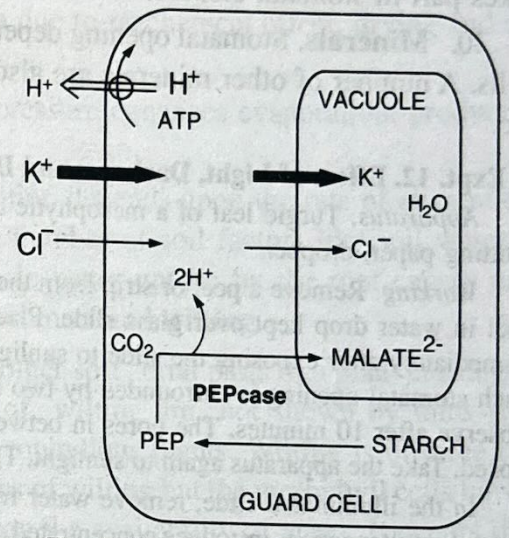


Fig. 11.37. Role of K^+, Cl^- and malate in increasing osmotic concentration (decreasing water potential) of guard cells.

Factors Affecting Stomatal Movements

Stomatal movements are influenced by a number of environmental factors like light, temperature, humidity, water availability and CO_2 concentration. Internal or endogenous factors include growth hormones, organic acids, K^+, Cl^- and H^+ ions.

1. **Light**. In the majority of plants the stomata open in light and close in darkness. The light intensity required for stomatal opening is quite low (250 ft candles in Tobacco). Even moon light is sufficient in some cases (Loftfield, 1921). Both red and blue parts of light are effective though the latter is slightly more effective (Mouravieff, 1958). However, in succulents or CAM plants (crassulacean acid metabolism), the stomata remain closed during daytime. They open only during dark, *e.g., Agave, Opuntia*, Pineapple.

2. **Temperature**. Q_{10} for stomatal opening is two. At 38°– 40°C, stomata can open in complete darkness, while at 0°C they remain closed even in continuous light. Normally high temperature above 30°C reduces stomatal opening in many species.

3. **Atmospheric Humidity**. In humid environment the stomata remain opened for longer periods while in dry environment they remain closed for longer periods.

4. **Water Availability**. Plants undergo water stress if availability of water is less than the rate of transpiration. Water stress (= water deficit = moisture deficit) brings about stomatal closure due to ABA and rise in DPD of epidermal cells.

5. **Mechanical Shock**. It causes closure of stomata.

6. **CO_2 Concentration**. Low CO_2 concentration usually induces opening of stomata while high CO_2 concentration closes the same. In some plants mere breathing over the leaves causes stomatal closure. However, guard cells are sensitive to CO_2 concentration only from their inner side (*i.e.*, concentration in the leaf interior). Stomata of a plant transferred to dark CO_2 free environment will remain closed but they will open in light when internal CO_2 is utilised.

7. **Oxygen**. It is essential for opening of stomata (Lougnet, 1972).

8. ***p*H**. Rise in *p*H is known to be required for opening of stomata while a fall in *p*H induces closure of stomata.

9. **Growth Hormones**. Cytokinins are essential for opening of stomata while abscisic acid takes part in stomatal closure.

10. **Minerals**. Stomatal opening depends upon availability of K^+ ions from adjacent epidermal cells. A number of other minerals are also essential for stomatal movements, *e.g.*, P, N, Mg, Ca, etc.

Expt. 12. Effect of Light, Darkness and Dehydration on Stomatal Movements.

Apparatus. Turgid leaf of a mesophytic dicot, water, strong sucrose or salt solution, slide, cover slip, blotting paper, dropper.

Working. Remove a peel or strip from the lower surface of mesophytic leaf exposed to sun. Mount the peel in water drop kept over glass slide. Place a cover slip over it. Study the peel under the microscope immediately after exposing the slide to sunlight. The peel will be seen to have a number of open stomata. Each stomatal opening is surrounded by two bent kidney-shaped guard cells. Take the apparatus to shade. Observe after 10 minutes. The pores in between the gaurd cells have disappeared, that is, the stomata get closed. Take the apparatus again to sunlight. The stomata open again.

In the illuminated slide, remove water from below the cover slip from one end by means of blotting paper. Simultaneously, introduce concentrated sucrose or salt solution from the other end by means of dropper. When the whole of water has been replaced by concentrated solution, observe under the microscope. The stomata get closed though they are still exposed to light. Replace sucrose solution with water. The stomata open again. Allow the water to get dried. It closes the stomata.

Results. (i) Opening of stomata in light and their closing in darkness shows that light is essential for the opening of stomata. (ii) Strong sucrose or salt solution and dehydration have the same effect. The guard cells lose their turgidity and the stomata get closed.

Precautions. (i) The strip or peel should be carefully removed so that the shock effect is minimum. (ii) Keep the lower end of leaf dipping in water before use. (iii) The strip should not be left out to dry. It must be immediately dipped in water.

Factors Affecting Transpiration

External Factors (Environmental Variables)

1. **Relative Humidity**. Relative humidity is the percentage of water vapour present in the air at a given time and temperature relative to the amount required to be present to make the air saturated at that temperature. The rate of transpiration is inversely proportional to the relative humidity, *i.e.*, the rate of transpiration is higher when the relative humidity is lower and lower when the relative humidity is higher. It is because the leaf interior has a nearly saturated air in its intercellular spaces. Relative humidity of the atmospheric air governs its vapour pressure deficit or DPD or water potential. Since DPD of atmospheric air is higher at low relative humidity, more of water vapours will diffuse out of the leaf interior as compared to high RH when DPD is lower.

2. **Atmospheric Temperature**. A high temperature opens stomata even in darkness. Besides producing a heating effect, it lowers the relative humidity of the air and increases vapour pressure inside transpiring organ. For 10°C rise in atmospheric temperature vapour pressure inside leaves doubles while relative humidity decreases by 50%. Consequently, rate of transpiration increases. However, leaf temperature does not rise corresponding to rise in atmospheric tempera-

ture due to cooling effect of transpiration. Very high temperature may cause desiccation and closure of stomata. Very low temperature also closes the stomata and hence decreases the rate of transpiration.

3. **Light**. In the majority of plants stomata open in the presence of light and close in darkness. A strong light further increases transpiration probably due to its heating effect. Because most of the transpiration occurs through stomata, the rate of transpiration is quite high in light. It falls down appreciably in the darkness.

4. **Air Movements** (Wind). Transpiration is lower in the still air because water vapours accumulate around the transpiring organs and reduce the DPD of the air. The movement of the air increases the rate of transpiration by removing the saturated air around the leaves. Upto 20–30 km/hr the rate of transpiration increases with the wind velocity. A wind velocity of 40–50 km/hr decreases transpiration by closing the stomata due to mechanical effect, drying and cooling of the transpiring organs.

5. **Atmospheric Pressure**. Low atmospheric pressure enhances evaporation, produces air currents and increases the rate of transpiration.

6. **Availability of Water**. The rate of transpiration depends upon the rate of absorption of soil water by roots. This is further influenced by a number of soil factors like soil water, soil particles, soil temperature, soil air, etc. A decrease in water uptake by the root causes partial dehydration of the leaf cells resulting in closure of stomata and **wilting**.

Wilting. It is the loss of turgidity of leaves and other soft aerial parts of a plant causing their drooping, folding and rolling. The symptoms of wilting are not shown by thick-walled tissues. Therefore, they are less conspicuous in sclerophyllous plants. Wilting is of three types: (i) **Incipient Wilting**. There are no external symptoms of wilting but the mesophyll cells have lost sufficient water due to transpiration being higher than the availability of water. It occurs during midday for a brief period in almost all plants even when sufficient water is present in the soil. (ii) **Temporary Wilting** (Transient Wilting). It is the temporary drooping down of leaves and young shoots due to loss of turgidity during noon. At this time the rate of transpiration is maximum. The rate of water absorption is less due to shrinkage of roots and depletion of water around the root hairs. Lower leaves show wilting earlier than the upper ones. Temporary wilting is corrected only after the rate of transpiration decreases in the afternoon accompanied by replenishment of water around the root hairs. (iii) **Permanent Wilting**. A permanent wilting is that state in the loss of turgidity of leaves when they do not regain their turgidity even on being placed in a saturated atmosphere. It occurs when the soil is unable to meet the requirement of plant for transpiration. Water is present in the soil largely in unavailable form (echard). At permanent wilting percentage (PWP) or coefficient (PWC) the soil contains 10–15% water depending upon its texture (about 10% in loam soil). After permanent wilting the plant dies.

Internal or Plant Factors

1. **Leaf Area** (Transpiring Area). A plant with large leaf area will show more transpiration than another plant with less leaf area. However, the rate of transpiration per unit leaf area decreases in a canopy due to density of foliage, shading effect and decrease of air movement inside the canopy.

2. **Leaf Structure**

(a) *Thickness of Cuticle*. Cuticular transpiration decreases with the thickness of cuticle and cutinisation of epidermal walls.

(b) *Number and Position of Stomata*. Because most of the transpiration takes place through the stomata, their number influences the rate of transpiration. Most dicots have stomata re-

stricted to lower surface while the isobilateral monocot leaves possess equal number of stomata on both the surfaces.

(c) *Sunken Stomata*. The sunken stomata are device to reduce the rate of transpiration by providing an area where little air movement occurs.

(d) *Stationary Layer and Hair*. The hair insulate the surface of the leaf from air currents and air temperature. They hold a **stationary layer** of air (also called boundary layer). The thicker the boundary or stationary layer, the lower is the rate of transpiration. It is because the leaf will first lose water to stationary layer and from there it would travel to the outside.

(e) *Mesophyll*. Compact mesophyll (as having more of palisade tissue and fewer intercellular spaces) reduces transpiration while a loose mesophyll (having more of spongy tissue and larger intercellular spaces) increases transpiration.

(f) *Leaf Modifications*. Formation of prickles, leaf spines, scaly leaves, phyllodes, phylloclades (instead of leaves), are all modifications found in xerophytes to reduce transpiration. In xerophytes the leaves are also smaller (to reduce the effect of heating) and leathery (to prevent wilting).

3. **Root/Shoot Ratio**. A low root/shoot ratio decreases the rate of transpiration while a high ratio increases the rate of transpiration. The latter is due to the fact that an extensive root system is more efficient in water uptake from soil. Increased availability of water also increases transpiration.

4. **Mucilage and Solutes**. They decrease the rate of transpiration by holding water tenaciously.

Significance of Transpiration

Advantages

1. **Ascent of Sap**. Ascent of sap mostly occurs due to transpiration pull exerted by transpiration of water. This pull also helps in absorption of water.

2. **Removal of Excess Water**. It has been held that plants absorb far more amount of water than is actually required by them. Transpiration, therefore, removes the excess of water.

3. **Cooling Effect**. Radiant heat falling on the plants increases their temperature which may be dangerous to the plants. Transpiration, by evaporating water, lowers down their temperature by 10°–15°C.

4. **Mechanical Tissue**. The development of mechanical tissue, which is essential for providing rigidity and strength to the plant, is favoured by the increase in transpiration.

5. **Distribution of Mineral Salts**. Mineral salts are mostly distributed by rising column of sap.

6. **Increasing Concentration of Mineral Salts**. The sap absorbed from the soil contains low concentration of mineral salts. The loss of water through transpiration increases the concentration of mineral salts in the plant.

7. **Root System**. Transpiration helps in better development of root system which is required for support and absorption of mineral salts.

8. **Quality of Fruits**. The ash and sugar content of the fruit increases with the increase in transpiration.

9. **Resistance**. Excessive transpiration induces hardening and resistance to moderate drought.

10. **Turgidity**. Transpiration maintains the shape and structure of plant parts by keeping cells turgid.

11. **Photosynthesis**. Transpiration supplies water for photosynthesis. As water evaporates

through the stomata, it results in pulling of water, molecule by molecule into the leaf from the xylem.

Disadvantages

1. **Wilting**. Wilting or loss of turgidity is quite common during noon due to transpiration being higher than the rate of water absorption. Wilting reduces photosynthesis and other metabolic activities.

2. **Reduced Growth**. Transpiration reduces availability of water inside the plant. Water deficit decreases growth and hence the plant gives a stunted appearance.

3. **Reduced Yield**. As reported by Tumarov (1925), a single wilting reduces growth by 50%. It is because decreased availability of water inside the plant checks meristematic activity and hence the formation of flowers, fruits and seeds.

4. **Abscisic Acid**. Water stress produces abscisic acid. Abscisic acid prevents several plant processes and promotes abscission of leaves, flowers and fruits.

5. **Wastage of Energy**. Since 98–99% of absorbed water is lost through transpiration, the energy used in absorption and conduction of water goes waste.

6. **Modifications**. In order to reduce transpiration during critical periods, the plants produce several types of modifications— thick cuticle, hair, prickles, spines, thorns, sunken stomata, phylloclades, cladodes, etc.

Nevertheless transpiration cannot be checked. Stomatal transpiration will always occur whenever stomata are open for gaseous exchange (so essential for photosynthesis and respiration). Similarly cuticular and lenticular types of transpiration cannot be checked as there is no method of their control. Hence transpiration is regarded as a **necessary evil** (Curtis, 1926) or **unavoidable evil** (Steward, 1959).

Transpiration and Photosynthesis— a compromise (Water Requirement)

The amount of water transpired per unit of dry matter manufactured by a plant is called **water requirement, transpiration ratio** or efficiency of transpiration (Lowes, 1850). It is minimum for crassulacean or succulent plants, moderate in C_4 plants and maximum in C_3 plants. The common value is 300 – 600. In CAM plants, it is about 50. C_3 plants transpire the maximum. Humidity of rain forests is due to large scale water lost by plants. It results in condensation and local rain. C_3 plants lose 600 – 900 grams of water for one gram of dry matter synthesized. It is because they have high sponginess of their mesophyll tissue due to presence of fine spaces in between the palisade cells and larger spaces in between the spongy parenchyma cells.

C_4 plants have evolved a strategy to maximise availability of CO_2 and minimise the water loss. Their transpiration ratio is 300. C_4 plants are twice as efficient as C_3 plants in terms of fixing carbon. However, a C_4 plant loses only half as much water as a C_3 plant for the same amount of CO_2 fixed. CAM plants do not open their stomata during the day. They also store water. The plants absorb and store carbon dioxide during night when transpiration loss is minimum. The absorbed CO_2 is used in photosynthesis during the daytime. The value indicates the requirement of irrigation and rain. In areas where irrigation is not adequate and the rainfall is also not heavy, those crops and plants can be grown which have low water requirement. Thus Sorghum, Bajra and Ragi are useful for growth in these rainfed crop lands. The trees include *Dalbergia sisso*, Margosa (Neem), *Acacia, Prosopis*. When irrigation is assured, the suitable crops are Tomato, Sugarcane and Rice. Areas with good rainfall may be used for growth of Bamboo, Rose-wood, Willow, Teak, Arecanut, Coconut, Coffee and Tea.

Transpiration – a price paid for photosynthesis

Most of the plant physiologists hold the view that transpiration is a price which the plant pays for photosynthesis. As the stomata open in the light for gaseous exchange (CO_2 for photosynthesis and O_2 for respiration) water vapours escape side by side. When stomata are closed in dark, loss of water is minimum through transpiration. This means that transpiration occurs alongwith photosynthesis. For this reason, it is said that transpiration is the price which the plant pays for photosynthesis.

Antitranspirants

During drought conditions the plants show wilting. According to Tumarov (1925) a single wilting reduces plant yield by 50%. In arid and unirrigated areas crop plants cannot be grown because of excessive transpiration and reduced water availability. *Substances that reduce the rate of transpiration are called antitranspirants.* Antitranspirants will maintain a favourable internal water balance even in cases of very low water availability. It will allow farmers to grow crops profitably in unirrigated areas and help foresters to plant trees even in extreme arid or desert areas. Antitranspirants are of two types, metabolic inhibitors and surface films.

Metabolic inhibitors reduce transpiration by reducing the stomatal opening for a period of two or more weeks without influencing other metabolic processes. The most promising of these inhibitors is phenyl mercuric acetate (PMA, 10^{-4}M). Another is abscisic acid (ABA or AbA).

Film forming chemicals check transpiration by forming a thin film on the transpiring surface. They are sufficiently permeable to carbon dioxide and oxygen to allow photosynthesis and respiration but prevent movement of water vapours through them. The important chemicals of this group are silicon emulsions, colourless plastic resins and low viscosity waxes. However, antitranspirants are still in experimental stage.

GUTTATION

The loss or excretion of water in the form of liquid droplets from the leaves and other parts of an uninjured or intact plant is called **guttation**. It was first studied by **Bergerstein** in 1887. All plants do not show guttation. It is restricted to about 345 genera of herbaceous and some woody plants. Common examples are found in Garden Nasturtium, Oat and other cereals, Balsam, Tomato, Cucurbits.

Expt. 13. Demonstration of Guttation

Apparatus. A well watered potted plant of Garden Nasturtium or Oat, a bell jar, glass slab, vaseline.

Place a well watered potted plant of Garden Nasturtium or Oat under a bell jar over a flat surface preferably a glass slab. Seal the edges of the bell jar by vaseline. Within an hour small droplets of liquid water will be observed at the leaf margins (Garden Nasturtium, Fig. 11.38A) or leaf tips (Oat, Fig. 11.38 B).

The guttated liquid is never pure water. It contains 0.6–2.5 gm/litre of solutes— both organic (carbohydrates, organic acids, amino acids, enzymes) and inorganic (Ca^{2+}, Mg^{2+}, K^+, Na^+, CO_3^{2-}, SO_4^{2-}, Cl^-). Evaporation of guttated liquid will leave the solutes on the surface of the leaf in the form of a white crust (another reason for the latter is excretion of salts in some halophytes). Guttation usually occurs during periods of active growth when conditions favour more water absorption and less transpiration. Such conditions are found in humid tropical areas, rainy seasons and late spring in temperate areas. Guttation takes place either at night or early in the morning. Dry soils, poorly aerated soils, heavily salted or mineral deficient soils and the atmospheric conditions promoting transpiration inhibit guttation.

Guttation drops can easily be mistaken for dew drops because both occur in the morning. However, dew generally does not fall on cloudy nights. Further guttation drops are restricted to tips or margins of the leaves while dew drops are found all over the plant and even the soil.

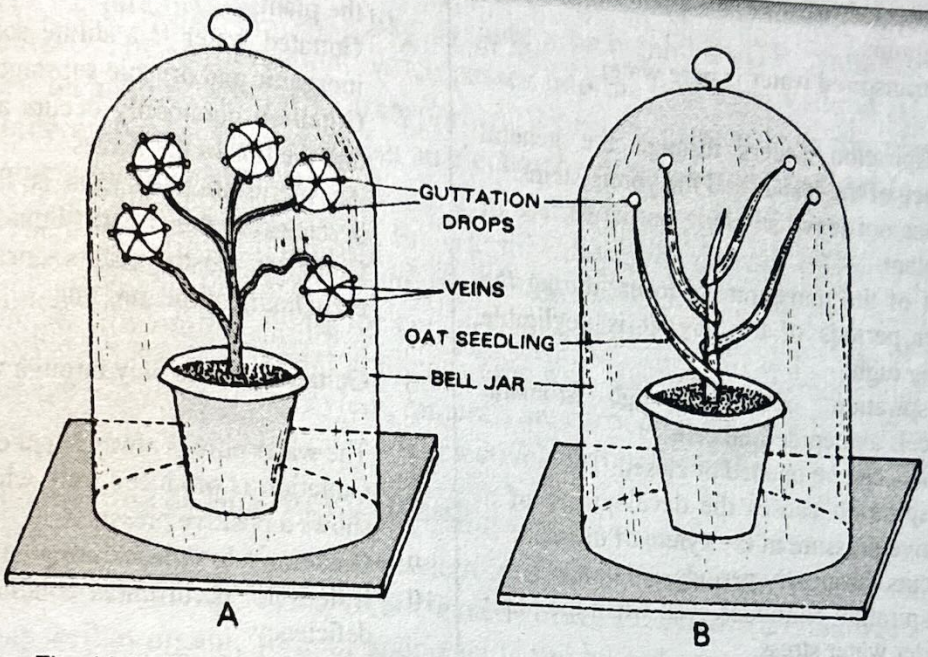


Fig. 11.38. Demonstration of guttation in A, Garden Nasturtium; B, Oat.

Guttation takes place through special structures called **hydathodes** (Fig. 11.39). They are usually found on the margins and tips of the leaves. Each hydathode consists of a group of loosely arranged achlorophyllous or colourless and parenchymatous cells called **epithem**. It lies over the tip of a vascular strand and communicates with the outside through a permanent pore in the epidermis called **water pore** or **water stoma**. The term hydathode is also applied to water pore. Exudation of liquid from the water pore or stoma is due to the development of a positive pressure in the xylem present in the vein ending. The pressure forces the liquid out through the hydathode. The epithem cells are specialized cells (called transfer cells) which help in absorbing a good percentage of inorganic and organic solutes present in the exudate. However, a part of these solutes do come out of the hydathode alongwith the liquid.

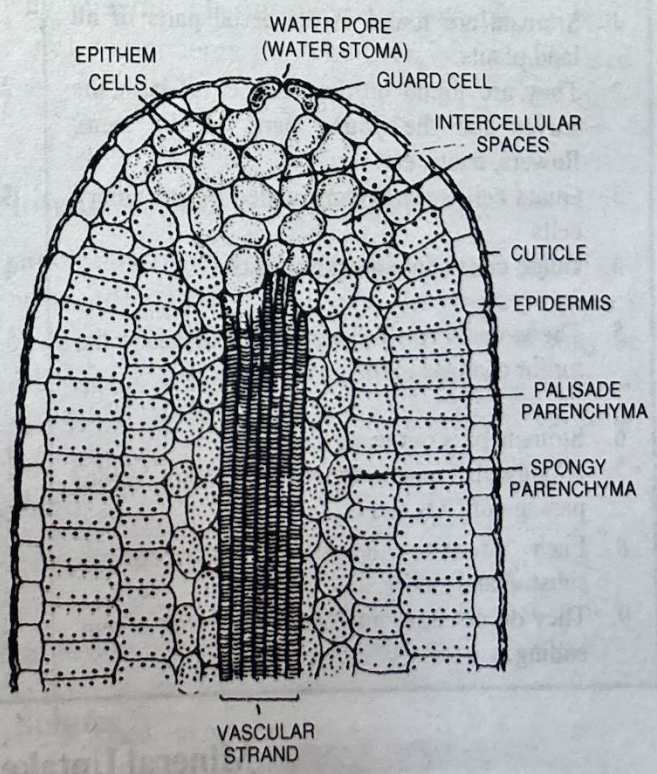


Fig. 11.39. Section of leaf showing hydathode.

Bleeding

It is the exudation of sap or watery solution from the cut or injured parts of the plant, *e.g., Agave, Acer, Vitis*, Toddy Palm. It occurs due to root pressure, phloem pressure, local pressure in xylem (stem pressure) and latex or resin.

Differences between Transpiration and Guttation

Transpiration	*Guttation*
1. It is the loss of water by a plant in the form of vapours.	1. Guttation is the loss of liquid droplets from the plant.
2. The transpired water is pure water.	2. Guttated water is a dilute solution of both inorganic and organic substances.
3. Transpiration occurs through the general surface of the leaves and the young stems.	3. Guttation commonly occurs at the margins and the tips of the leaves.
4. It does not leave anything on the surface of the plant.	4. An incrustation of salts is formed on the surface after the guttated liquid evaporates.
5. Most of the transpiration occurs during the hotter periods of the day. It is negligible during night.	5. Guttation mostly occurs during night and early hours of the morning.
6. Transpiration occurs through stomata, lenticels and epidermal cells.	6. Guttation occurs only through water pores.
7. Stomata can be opened or closed.	7. The water pore is always kept open.
8. Transpiration causes the development of a negative pressure in the xylem of the plant.	8. Guttation is produced only when the xylem shows a positive pressure.
9. It occurs during dry periods.	9. Guttation takes place during humid periods.
10. Transpiration continues even when the plant is under water stress.	10. It does not occur under conditions of water deficiency.
11. Excessive transpiration produces wilting.	11. Excessive guttation does not cause loss of turgidity.

Differences between Stomata and Hydathodes

Stomata	*Hydathodes*
1. Stomata are found in the aerial parts of all land plants.	1. Hydathodes occur on the leaves of only a few plants.
2. They are found on the surfaces of both the leaves and the young parts of the stem, flowers, fruits, etc.	2. Hydathodes occur on the margins and tips of the leaves.
3. Guard cells may be surrounded by subsidiary cells.	3. Subsidiary cells are absent.
4. Guard cells contain chloroplasts.	4. Cells bordering a water pore are usually achlorophyllous.
5. The stomata can be opened or closed by the turgor changes in the guard cells.	5. Hydathodes possess permanent pores because the guard cells surrounding them are immobile.
6. Stomata pass out water vapours.	6. Haydathodes send out liquid water.
7. Alongwith water vapours, stomata allow passage of CO_2 and O_2.	7. Small quantities of solutes also pass out dissolved in guttated liquid.
8. Each stomate leads internally to a substomatal cavity.	8. Hydathode possesses loosely arranged epithem cells below its pore.
9. They do not have any connection with a vein ending.	9. Hydathodes contain a vein ending.

Mineral Uptake by Roots

Plants obtain their supply of carbon and most of their oxygen from CO_2 of atmosphere, hydrogen from water while the rest are minerals which are picked up individually from the soil.

Minerals exist in the soil as **ions** which cannot directly cross the cell membranes. The concentration of ions is some 100 times more in root interior than in the soil. Therefore, all minerals can not be passively absorbed. The movement of ions from soil to interior of root is against concentration gradient and requires an **active transport**. Specific **ion pumps** occur in the membrane of root hairs. They pump mineral ions from soil to cytoplasm of epidermal cells of root hairs. Energy is provided by ATP. Respiratory inhibitors like cyanide which inhibit ATP synthesis, generally reduce the ion uptake. The small amount which passes into the root even without ATP, must be through a passive technique. For active transport, ATPases are present over the plasma membranes of root epidermal cells. They establish an **electrochemical proton gradient** for supplying energy for movement of ions. The ions are again checked and transported inwardly by **transport proteins** present over the endodermal cells. Endodermis allows the passage of ions inwardly but not outwardly. It also controls the quantity and type of ions to be passed into xylem. Inward flow of ions from epiblema to xylem is along the concentration gradient. The collection of ions in the xylem is responsible for water potential gradient in the root that helps in osmotic entry of water as well as its passage to xylem. In the xylem, minerals are carried up alongwith the flow of xylem solution. In leaves the cells absorb the minerals selectively through membrane pumps (Fig. 11.21).

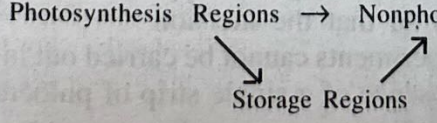
Translocation of Mineral Ions in the Plant

Though it is generally considered that xylem transports inorganic nutrients while phloem transports organic nutrients, the same is not exactly true. In xylem sap, nitrogen travels as inorganic ions, as well as organic form of amino acids and related compounds. Small amounts of P and S are passed in xylem as organic compounds. There is also exchange of materials between xylem and phloem. Therefore, mineral elements pass up xylem in both inorganic and organic form. They reach the area of their sink, namely young leaves, developing flowers, fruits and seeds, apical and lateral meristems and individual cells for storage. Minerals are unloaded at fine vein endings through diffusion. They are picked up by cells through active uptake.

There is remobilization of minerals from older senescing parts. Nickel has a prominent role in this activity. The senescing leaves send out many minerals like nitrogen, sulphur, phosphorous and potassium. Elements incorporated in structural components are, however, not remobilised. *e.g.*, calcium. The remobilised minerals become available to young growing leaves and other sinks.

Phloem Transport : Flow from Source to Sink

It is the long distance movement of organic substances from the **source** or supply end (region of manufacture or storage) to the region of utilization or **sink**. But the source and sink may be reversed depending on the season or need of the plants. Sugar stored in roots may be mobilised to become a source of food in the early spring when the buds of trees act as sink and require energy for their growth and development. Since the source–sink relationship is variable, the direction of movement of organic solutes in phloem can be upwards or downwards *i.e.*, *bidirectional* (c.f. unidirectional upwards in xylem).



Directions of Translocation of Organic Solutes

Translocation of organic solutes can occur in the following directions :

1. **Downward Translocation.** It is the most common mode of translocation. The leaves manu-

facture food in excess of their own requirement. The excess food comes out of leaves and is translocated in the downward direction to stem (for storage, metabolism, maintenance of its cells and secondary growth, if any) and root system (for storage, growth, metabolism and maintenance).

2. **Upward Translocation**. In deciduous plants renewal of growth and development of new foliage are dependent upon upward transport of food from reserves present in the roots and stems. Growth of the stem apices, formation of flowers, fruits, etc. require the movement of assimilates from leaves in an upward direction.

3. **Lateral Translocation**. It is little except when source and sink lie on the opposite sides (Peel, 1964).

4. **Bidirectional Translocation**. Rabideau and Burr (1945) found that labelled carbohydrates moved out of the leaves in both upward and downward directions. The two types of translocation are believed by many workers to occur in different sieve tubes.

Differences between Diffusion and Translocation

Diffusion	*Translocation*
1. It occurs in all directions through the available space.	1. It is directional movement of materials.
2. A vascular tissue is not required.	2. It occurs inside vascular tissues.
3. Diffusion is a slow process.	3. Translocation is a rapid process.
4. Diffusion occurs at the particulate level.	4. Translocation is passage of materials in bulk.

Pathway of Translocation

The most common organic nutrient translocated in plants is sucrose. The channels of transport are sieve tubes (in flowering plants) and sieve cells (in nonflowering vascular plants) of phloem. It was proved for the first time by Czapek (1897). The evidences are as follows :

1. There are only two paths for long distance transiocation, tracheary elements and sieve tubes. The former are dead while the latter are living. Translocation of organic solutes seems to be through sieve tubes because it is inhibited by steam girdling which kills living cells.

2. In **girdling** or **ringing** experiments (Malpighi, 1675), a ring of bark is cut from the stem. It also removes phloem. Nutrients collect above the ring where the bark also swells up and may give rise to adventitious roots (Fig. 11.40). Growth is also vigorous above the ring. The tissues below the ring not only show stoppage of growth but also begin to shrivel (Roots can be starved and killed if the ring is not healed after some time. Killing of roots shall kill the whole plant) clearly showing that bark or phloem is involved in the movement of organic solutes which occurs in one direction, *i.e.*, towards root.

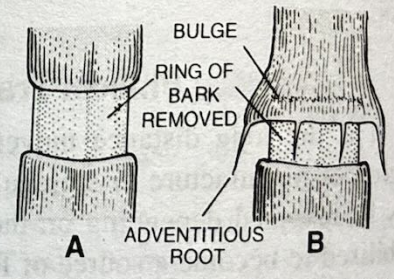


Fig. 11.40. Girdling of tree trunk to show that organic nutrients accumulate in the bark above the girdle where a bulge is also produced.

Girdling experiments are performed in fruit trees to make more food available to fruits. However, the rings are kept narrow and cambium is not touched so that the incision heals up after some time. (Girdling experiments cannot be carried out in monocots and dicots with bicollateral bundles because of the absence of a single strip of phloem).

3. Mason and Maskell (1928) inserted a wax paper between phloem and xylem. Parts of the bark were also removed except for a narrow strip. They found evidence that the organic solutes passed through the narrow strip of bark containing the phloem.

4. By means of **aphid stylets**, Weatherley *et al* (1959) found that sieve tubes contained a concentrated solution of organic substances under a pressure.

5. Radio-autographs show that assimilates with incorporated radioactive elements pass out of the leaves and travel towards the sink ends through phloem.

6. Sieve tubes contain a high organic solute content— 5–10% soluble carbohydrates (mostly surcose), about 1% nitrogenous compounds (mostly amino acids), organic acids besides traces of hormones and other organic solutes. Sucrose is most suitable form of carbohydrate translocation as it is nonreducing and chemically stable. It does not react with other substances during translocation.

7. Tonoplast is absent in sieve tube cells so that cytoplasm is in direct contact with vacuolar contents.

8. Sieve tube cytoplasm can tolerate high concentration of solutes without being plasmolysed.

9. Cytoplasm of one sieve tube cell is continuous with that of the adjacent sieve tube cells through sieve plates so as to form continuous filaments. The centre of sieve tube cells is empty with cytoplasmic strands being peripheral.

10. Sieve tube cells possess granules and filaments of P-protein with ATP-ase activity.

11. Relatively large amounts of organic solutes are translocated. The rate of translocation of organic nutrients is such that a sieve tube must be refilled 3–10 times per second (Zimmermann, 1964). Crafts and Lorenz (1944) found that a pumpkin fruit receives 5500 gm of the organic solution in 33 days with a rate of 0.61 gm of dry weight or translocation of 110 cm per hour.

12. Lateral movement from phloem to living cells or from source to phloem occurs through transfer cells and symplasm.

Mechanism of Phloem Translocation

Several theories have been put forward to explain the mechanism of translocation of organic nutrients through the phloem *e.g.*, diffusion, activated diffusion, protoplasmic streaming, interfacial flow, electrosmosis, transcellular strands, contractile proteins, mass flow. The important ones are as follows :

1. **Cytoplasmic Streaming Hypothesis**. It was put forward by de Vries (1885) and later developed by Curtis (1929–35). The hypothesis considers the transport to take place by combination of two forces, diffusion and cytoplasmic streaming. Cytoplasmic streaming carries organic solutes or food materials from one end to the

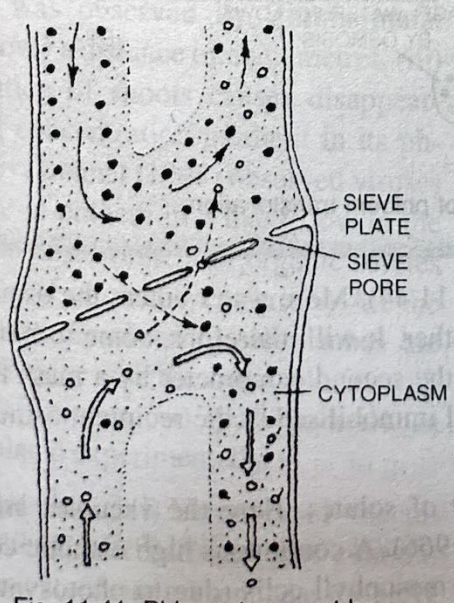


Fig. 11.41. Phloem transport by cytoplasmic streaming and diffusion.

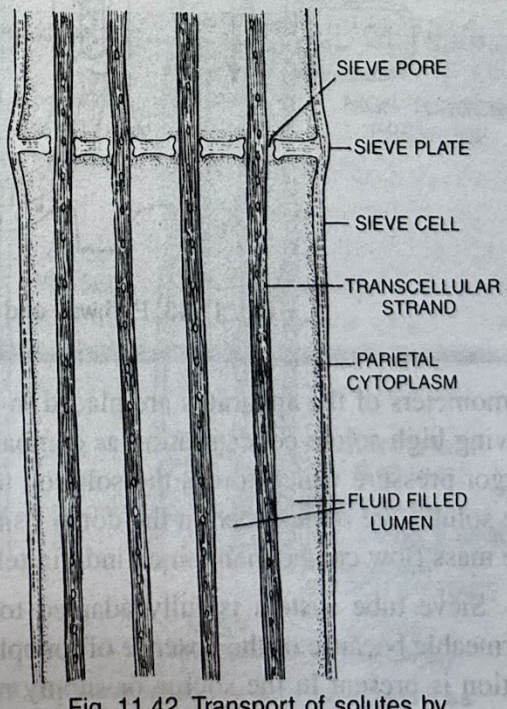


Fig. 11.42. Transport of solutes by transcellular strands.

other end of a sieve tube cell from where they difuse according to their concentration gradients to an adjacent sieve tube cell through the sieve plate (Fig. 11.41). The hypothesis can explain bidirectional movement of substances in the same sieve element. The important drawbacks of the theory are (i) The rate of cytoplasmic streaming is too slow to account for phloem transport (3 cm/hr as compared to 50–150 cm/hr of phloem transport). (ii) Though Thaine (1954) has observed cytoplasmic streaming to occur in some mature sieve tubes, it is normally absent in them. (iii) Phloem exudate does not contain cytoplasm.

2. **Transcellular Streaming Hypothesis** (Fig. 11.42). The hypothesis has been put forward by Thaine (1962, 1969). It believes that sieve tubes possess tubular strands which are continuous from one tube cell to the other through sieve pores. The tubular or transcellular strands show a sort of peristaltic movement which helps in the passage of organic substances. The transcellular strands have, however, not been observed in sieve tubes.

3. **Mass Flow or Pressure Flow Hypothesis**. It was put forward by Munch (1927, 1930). According to this hypothesis, organic substances move from the region of high osmotic pressure to the region of low osmotic pressure in a mass flow due to the development of a gradient of turgor pressure (Fig. 11.43). This can be proved by taking two interconnected osmometers, one with high solute concentration and the other with little osmotic concentration. The two

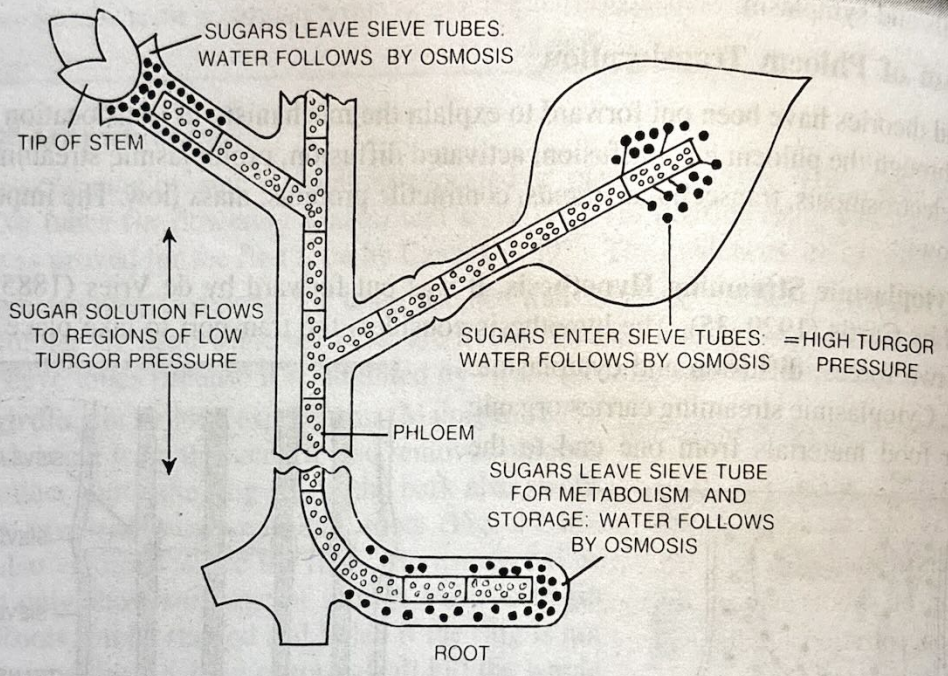

SUGARS LEAVE SIEVE TUBES: WATER FOLLOWS BY OSMOSIS
TIP OF STEM
SUGAR SOLUTION FLOWS TO REGIONS OF LOW TURGOR PRESSURE
SUGARS ENTER SIEVE TUBES: WATER FOLLOWS BY OSMOSIS
=HIGH TURGOR PRESSURE
PHLOEM
SUGARS LEAVE SIEVE TUBE FOR METABOLISM AND STORAGE: WATER FOLLOWS BY OSMOSIS
ROOT

Fig. 11.43. Pathway and mechanism of phloem translocation.

osmometers of the apparatus are placed in water (Fig. 11.44). More water enters the osmometer having high solute concentration as compared to the other. It will, therefore, come to have high turgor pressure which forces the solution to pass into the second osmometer by a mass flow. If the solutes are replenished in the donor osmometer and immobilised in the recipient osmometer, the mass flow can be maintained indefinitely.

Sieve tube system is fully adapted to mass flow of solutes. Here the vacuoles are fully permeable because of the absence of tonoplast (Esau, 1966). A continuous high osmotic concentration is present in the source or supply region, *e.g.*, mesophyll cells (due to photosynthesis). The organic substances present in them are passed into the sieve tubes through their companion cells by an active process. A high osmotic concentration, therefore, develops in the sieve tubes

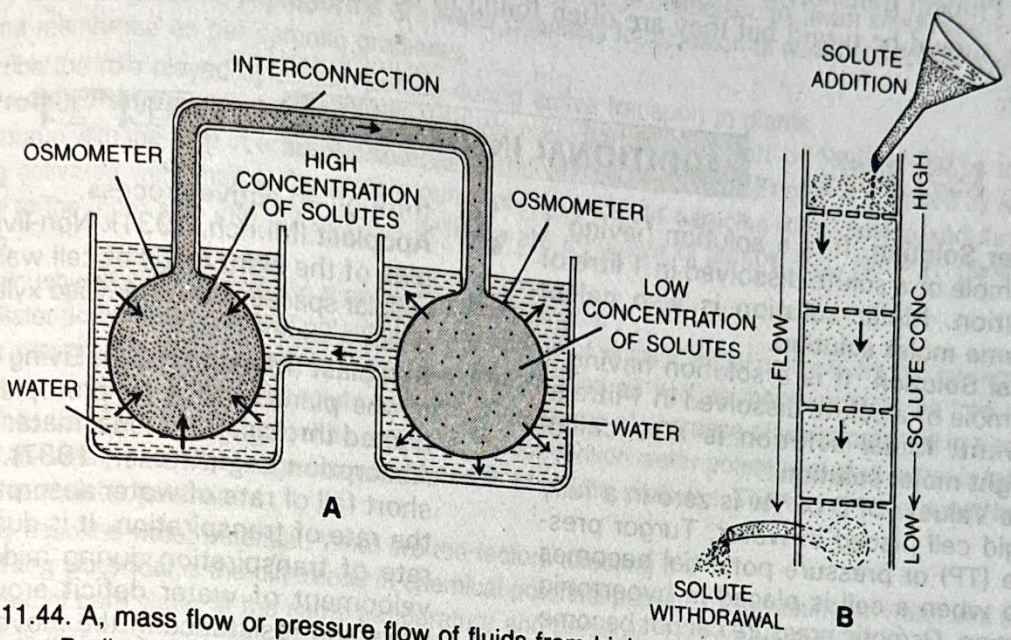


Fig. 11.44. A, mass flow or pressure flow of fluids from high to lower osmotic or turgor pressure. B, diagrammatic representation of continuous flow of solutes in one direction.

of the source. The sieve tubes absorb water from the surrounding xylem and develop a high turgor pressure (Fig. 11.45). It causes the flow of organic solution towards the area of low turgor pressure. A low turgor pressure is maintained in the sink region by converting soluble organic substances into insoluble form. Water passes back into xylem.

Evidences. (i) Sieve tubes contain organic solutes under a pressure because an injury causes exudation of solution rich in organic solutes. (ii) Direction of flow of organic solutes is always towards concentration gradient. A fall of 20% concentration was observed by Zimmermann (1957) over a distance of eight metres. (iii) Defoliation of shoots causes disappearance of concentration gradient in its phloem. (iv) Bennet (1937) observed viruses to move in phloem in a mass flow in the direction of movement of organic solutes at a rate of about 60 cm/hr. (v) All the substances dissolved in sieve tubes are found to move with the same velocity with minor differences. (vi) The hypothesis can be simulated experimentally.

Objections. (i) Vacuoles of the adjacent sieve tube cells are not continuous. The cytoplasm present near the sieve plates exerts resistance to the mass flow. (ii) Catalado *et al* (1972) have observed

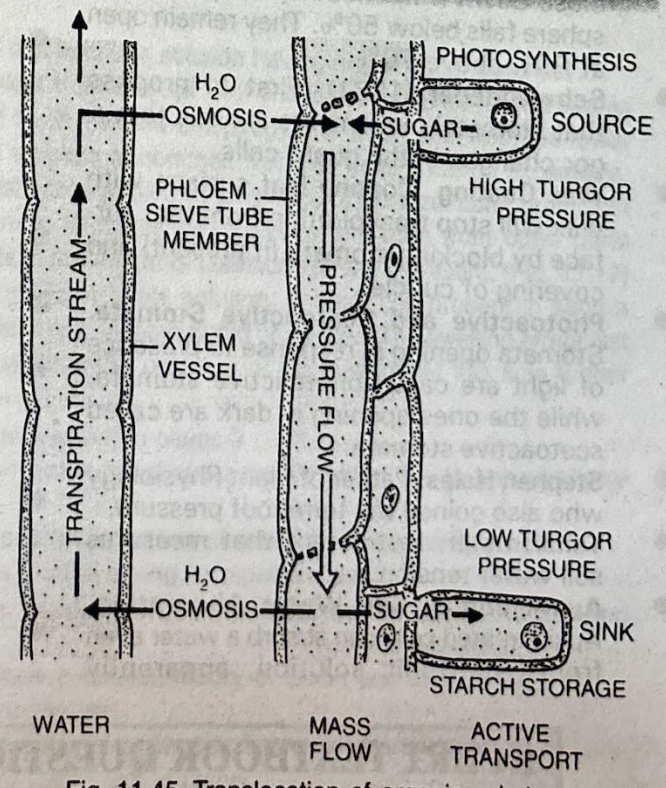


Fig. 11.45. Translocation of organic substances (assimilates) according to mass flow or pressure flow hypothesis.

that the rate of flow of water (72 cm/hr) and solutes (35 cm/hr) to be different in the same sieve tube. (iii) Phloem transport is not influenced by water deficit. (iv) The cells at the source end of mass flow should be turgid but they are often found to be flaccid in case of germinating tubers, corms, etc.

ADDITIONAL INFORMATION

- **Molar Solution**. It is a solution having 1 gm mole of a solute dissolved in 1 litre of solution. Molar solution is also called **volume molar solution**.
- **Molal Solution**. It is a solution having 1 gm mole of a solute dissolved in 1 litre of solvent. Molal solution is also called **weight molar solution**.
- **Zero Values**. DPD or Ψw is zero in a fully turgid cell placed in water. Turgor pressure (TP) or pressure potential becomes zero when a cell is placed in hypertonic solution. Osmotic pressure cannot become zero in a cell. It is zero only in case of pure water.
- **Matric Potential** (Imbibition Potential). It is the reduction in chemical potential of water due to imbibition by hydrophilic colloids.
- **Psychrometer**. It is an instrument for measuring both relative humidity and transpiration.
- **Relative Humidity and Stomata**. Stomata close down if relative humidity of atmosphere falls below 50%. They remain open at R.H. above 70%.
- **Schwendener** (1881). First to propose that stomatal movements are due to turgor changes in the guard cells.
- **Wax Coating**. Coating leaf surface with wax will stop transpiration from that surface by blocking stomata (if present) and covering of cuticle.
- **Photoactive and Scotoactive Stomata**. Stomata opening in response to presence of light are called photoactive stomata, while the ones opening in dark are called scotoactive stomata.
- **Stephen Hales**. Father of Plant Physiology who also coined the term root pressure.
- **Tensiometer**. Instrument that measures soil water tension.
- **Auxin and Active Water Absorption**. Auxin treated cells can absorb a water even from hypertonic solution, apparently through an active process.
- **Apoplast** (Munch, 1931). Non-living complex of the plant made of cell walls, intercellular spaces and water filled xylem channels.
- **Symplast** (Munch, 1931). Living complex of the plant formed by protoplasts connected through plasmodesmata.
- **Absorption Lag** (Kramer, 1937). It is the short fall of rate of water absorption over the rate of transpiration. It is due to high rate of transpiration during midday, development of water deficit around root hairs and resistance in the movement of water inside the plant.
- **Tensile Strength of Water**. It is the ability of water column to get stretched without breaking. The value is 45-207 atm (Dixon and Joly, 1894). Tensile strength is due to cohesive force amongst molecules of water and adhesion between water molecules and walls of xylem.
- **Atmometer**. It is an apparatus for demonstrating and measuring pull caused by evaporation of water from a porous pot.
- **Wilting and Water-logging**. In water-logged soils the plants often show wilting. It is caused by development of ethylene precursor by the roots (Bradford and Young, 1981) which reaching the shoot brings about wilted condition.
- **Potometer**. It is an apparatus for measuring the rate of transpiration.
- **Porometer**. It is an apparatus for knowing the relative sizes of stomata.
- **Cytoplasmic Streaming.** It is movement of cell cytoplasm in eukaryotes, *e.g., Hydrilla* leaf cells, *Tradescantia* (= Rhoeo) staminal hair.
- **Stomatal Index.** It is ratio of number of stomata to the total number of epidermal cells and stomata (E + S) per unit leaf area. It is fixed for a species.
- **The term** hydathode **is also applied to water pore.**

NCERT TEXTBOOK QUESTIONS WITH ANSWERS

1. What are the factors that affect the rate of diffusion ?

✓ (i) Density of the substance. (ii) Density or permeability of the medium. (iii) Temperature (iv) Diffusion pressure. (v) Distance.

2. What are porins ? What role do they play in diffusion ?
✓ **Porins** are proteins lined hydrophilic channels present in the outer membrane of plastids, mitochondria and some bacteria. They allow passage of large biomolecules, even small sized proteins as per diffusion gradient. **Aquaporins** are water channels for diffusion of water molecules across the plasma membrane as per osmotic gradients.

3. Describe the role played by protein pumps during active transport in plants.
✓ **Protein Pumps** are carrier proteins which take part in transport of solutes across the cell membrane with the help of energy even against concentration gradient. Energy is supplied by ATP. On being activated with energy, the protein pump picks up solute particles from outside and throw the same to the inner side into the cytoplasm. There are a number of pumps, *e.g.*, $Na^+ - K^+$ pump, Ca^{2+} pump.

4. Explain why pure water has the maximum water potential ?
✓ Water potential is chemical potential or free energy of water in molal unit volume in a system. Pure water has the maximum number of free water molecules as well as the amount of the free energy decreases with the addition of solute particles. The degree of decrease of water potential in a solution depends upon the number of solute particles. By convention water potential of pure water is taken as zero. Its value becomes negative with addition of solute particles. Therefore, pure water has the maximum water potential.

5. Briefly describe water potential. What are the factors affecting it ?
✓ **Water potential** is the difference in chemical potential per unit molal volume of water in a system and that of pure water at the same temperature and pressure. By convention water potential of pure water is taken as zero. Its value becomes negative in a solution as the solute particles reduce the chemical potential of water by decreasing its free energy.
Factors. (i) Solute potential (Ψs). (ii) Pressure potential Ψp. (iii) Matric potential (Ψm due to colloidal particles). (iv) Temperature. (v) Pressure (vi) Loss or gain of water.

6. What happens when a pressure greater than the atmospheric pressure is applied to pure water or a solution ?
✓ Pressure applied to pure water or a solution is a positive pressure that will increase the diffusivity of water whether in pure water or in solution. In solution it will reduce or prevent the entry of water from outside. If the solution is very dilute, pressure can cause reverse osmosis.

7. (a) With the help of well labelled diagrams, describe the process of plasmolysis in plants giving appropriate examples.
(b) Explain what will happen to a plant cell if it is kept in a solution having higher water potential ?
✓ (a) Plasmolysis is a shrinkage of protoplast from the cell wall under the influence of hypertonic solution. This can be observed by placing of fresh filament of *Spirogyra* or fresh peel from the lower surface of *Rhoeo (= Tradescantia)* in a 10% solution of common salt. The cells undergo exosmosis. Loss of water results in shrinkage of protoplast accompanied by shrinkage of cell size. Later protoplast will separate from the wall first at the corners (incipient plasmolysis) and then from other parts (evident plasmolysis) except for certain points in the region of plasmodesmata, if present. (Fig. 11.17)
(b) Higher water potentiai occurs in a hypotonic or dilute solution. A plant cell present in such a solution will absorb water due to endosomosis. It will become turgid or swollen. The swelling protoplast develops a wall pressure that becomes equal to water potential of the system. At this time further endosmosis stops.

8. What role does root pressure play in water movement in plants ?
✓ (i) Being a positive pressure, it meets the water deficit of the cells created due to transpirational loss.
(ii) Certain workes believe that root pressure helps in ascent of water in small-sized plants.
(iii) It dissolves and removes the air bubbles formed during transpiration pull.

9. Describe transpiration pull model of water transport in plants. What are the factors influencing transpiration ? How is it useful to plants ?
✓ **Transpiration Pull Model.** Describe cohesion-tension theory of Dixon and Joly (1894).
Factors Influencing Transpiration. Refer to the text.
Uses of Transpiration. Refer to the text advantages under significance of transpiration.

10. Discuss the factors responsible for ascent of xylem sap in plants.
✓ The various factors responsible for ascent of sap are as follows : (i) **Capillarity.** It is limited rise of water in narrow tubes or capillaries due to forces of cohesion amongst molecules of water and their property of adhesion to other substances. (ii) **Imbibition.** It is the ability of hydrophilic colloids to

attract and hold water on the surface and inside their interspaces. (iii) **Root Pressure.** It is positive pressure that pushes sap from below due to active absorption by root. (iv) **Transpiration Pull.** Transpiration in aerial parts brings the xylem sap under negative pressure or tension due to continuous withdrawal of water by them. Water column does not break due to its high tensile strength related to high force of cohesion and adhesion.

11. What essential role does the root endodermis play during mineral absorption in plants ?
✓ Endodermis has two essential roles in mineral absorption. (i) It regulates the movement of minerals passing into vascular strand due to presence of casparian strips. Minerals have to pass through symplast pathway and then special sets of carrier proteins and ion channels present in the plasma membrane of endodermal cells. (ii) Endodermis does not allow the flow of minerals back from vascular strand into cortex of root.

12. Explain why xylem transport is unidirectional and phloem transport bidirectional.
✓ Direction of transport is determined by the sink or area of utilisation of the material under transport. **Unidirectional Xylem Transport.** Xylem transport is unidirectional and upwards from roots to shoot tips. The force for upward movement develops in the aerial parts due to loss of water in transpiration. It creates a tension or negative pressure in the water column. The latter is, therefore, pulled upwards. **Bidirectional Phloem Transport.** Organic nutrients are loaded in the phloem in the region of manufacture (*e.g.*, leaves) or storage. It draws water into the area creating a high turgor pressure. A low turgor pressure exists in the area of utilisation of nutrients (*e.g.*, roots, shoot tips) because of regular withdrawal. Transport occurs both in the downward and upward directions from the leaves due to gradient of turgor pressure.

13. What causes the opening and closing of guard cells of stomata during transpiration ?
✓ Opening and closing of stomata occurs due to influx and efflux of K^+ ions into or out of guard cells. For details Refer to the text.

14. Differentiate between the following : (a) Diffusion and Osmosis, (b) Transpiration and Evaporation, (c) Osmotic Pressure and Osmotic Potential, (d) Imbibition and Diffusion, (e) Apoplast and Symplast pathways of movement of water in plants, (f) Guttation and Transpiration.
✓ (a) **Differences between Diffusion and Osmosis.** Refer to the text.
(b) **Differences between Transpiration and Evaporation.** Refer to the text.
(c) **Differences between Osmotic Pressure and Osmotic Potential.** Refer to the text.
(d) **Differences between Imbibition and Diffusion.** Refer to the text.
(e) **Differences between Apoplast and Symplast Pathway of Movement of Water in Plants.** Refer to the text.
(f) **Differences between Guttation and Transpiration.** Refer to the text.

15. How is mycorrhizal association helpful in absorption of water and minerals in plants ?
✓ Refer to the text under mycorrhizal water absorption.

16. Explain pressure flow hypothesis of translocation of sugars in plants.
✓ Refer to the text.

TEST QUESTIONS

One Mark Questions (With Answers)

1. Which of the following has highest water potential ?
(i) IM Salt solution (ii) IM Sugar solution (iii) Distilled water (iv) IM Sugar solution with 2–3 bars pressure.
✓ Distilled water.

2. Which fraction of soil water is available to plants for absorption by roots ?
✓ Capillary water

3. Expand DPD ?
✓ Diffusion Pressure Deficit .

4. What will happen if a plant cell is kept in solution of higher water potential ?
✓ Endosmosis.

5. What will happen if a plant cell is kept in hypotonic solution for some time ?
✓ Endosmosis.

6. A plant cell kept in certain solution got plasmolysed. What was the nature of the solution ?
✓ Hypertonic.

7. Why is energy required to develop root pressure ?

✓ Every activity requires energy. Root pressure develops due to activity of living cells of the root.

8. Define guttation ?
✓ The loss or excretion of water in the form of liquid droplets from the leaves and other parts of an uninjured oor intact plant is called **guttation**.
9. What are hydathodes ?
✓ Special structures found on margins and tips of leaves made of epithem cells and water pores through which guttation takes place.
10. What is atmometer ?
✓ It is an apparatus for demonstrating and measuring pull caused by evaporation of water from a porous pot.
11. If in an osmotic system, one chamber has a Ψ of –1000 kPa while the other has –500 kPa, which chamber has higher Ψ and what is it ?
✓ Chamber with –500 kPa. It has dilute solution.
12. What would be Ψ_p of a flaccid cell ?
✓ Zero.
13. What would be Ψ_p of a plasmolysed cell ?
✓ Negative.
14. Which organisms other than plants possess cell wall ?
✓ Bacteria, fungi, some protists.
15. Where are porins present ?
✓ Outer membrane of Gram negative bacteria, mitochondria and plastids.
16. How many types of aquaporins recorded ?
✓ 8 types.

One Mark Questions (Without Answers)

17. Fill in the blanks :
(a) The water potential of pure water is_____
(b) When plant absorbs the water from the soil, the water potential of the root cell is_____than the soil.
(c) Plants lose water by the process of_____and_____
(d) Loss of the water through the epidermis of aerial parts of the plant is reduced by_____
18. What are hydathodes ?
19. Which is the principal mineral cation in the extracellular fluid.
20. Name the pores through which guttation occurs.
21. Name the plant process carried by hydathodes.
22. Define osmosis.
23. A cell has OP of 10 bars and its TP is 6 bars, find its DPD ?
24. Who proposed K^+ hypothesis for opening and closing of stomata ?

Two Mark Questions (With sample Answers)

25. What is water potential ? Why is it negative in value ?
✓ It is difference in chemical potential per molal volume of water in a system and that of pure state at the same temperature and pressure. Water potential of pure water at normal temperature and pressure is zero. In solutions the value of water potential is always negative or less than zero.
26. A well watered potted herbaceous plant shows wilting in the afternoon of a dry sunny day. Why ?
✓ Wilting or loss of turgidity is quite common during noon due to transpiration being higher than the rate of water absorption.
27. When separated by a semipermeable membrane, water enters the sugar solution. What would you call the sugar solution — Osmotically active or inactive ?
✓ Osmotically active.
28. How root/shoot ratio affects transpiration ?
✓ A low root/shoot ratio decreases the rate of transpiration while a high ratio increases the rate of transpiration because of greater availability of water due to more extensive root system.
29. A plant is transpiring rapidly. Will it show root pressure also ?
✓ The rapidly transpiring plants do not show any root pressure. Instead a negative pressure is observed in most of the plants.
30. Trace the fate of molecule of water after it reaches the mesophyll cells.

Three Mark Questions (Short Answer Type)

31. What are guard cells ? Explain their role in regulating transpiration.
32. List the different factors that influence stomata.
33. Define hygroscopic and capillary waters ? Which is not available to plants and why ?

34. How do guard cells control opening and closing of stomata ?
35. How do Potassium ions regulate the opening and closing of stomata ?
36. List the three prominent theories to explain water translocation in trees. Describe the most accepted theory out of these.
37. Discuss the role of K^+ on the mechanism by which water moves into guard cells.
38. With the help of a labelled diagram describe briefly the closing and opening mechanism in stomata of plants such as common grass.
39. How do changes in TP help in opening and closing mechanism of stomata ?
40. Differentiate between TP and WP in plant cells. List any four ways in which turgidity serves a useful purpose in the plants.
41. Explain the significance of transpiration.
42. Differentiate between diffusion and osmosis.
43. Why do well watered plants transpire more during sunny and windy days than in cool and calm morning ? How transpiration is different from evaporation.

Five Mark Questions (Long Answer Type)

44. Discuss the importance of turgor pressure in life activities of plants.
45. Set up an experiment to demonstrate root pressure.
46. Write a note on hydathodes. Differentiate hydathodes from stomata.
47. What are the two kinds of interactions of water molecules that allow water to travel upward in plants? What other physical process aids in water transport to tops of trees ?
48. Explain why transpiration in higher plants is considered a necessary evil. *(HSB 2000, HSEB 2001)*
49. Define transpiration. Name the types of transpiration. Give the mechanism of transpiration giving V.S. of leaf.
50. How do potassium ions regulate the opening and closing of the stomata ?
51. Describe the active K^+ ion theory for stomatal opening.
52. What is ascent of sap ? Explain cohesion-tension theory for it.
53. What is transpiration ? Explain various factors affecting it.
54. Discuss role of transpiration pull in lifting water to the tops of tallest trees of the world.

Multiple Choice Questions (With Answers)

(1) Which one will reduce rate of transpiration ? (a) Rise in temperature (b) Increase in water uptake (c) Increase in wind velocity (d) Decrease in light intensity. *(MP PMT 1999)*

(2) Rate of transpiration is highest when (a) Soil is wet and air is dry (b) Soil is wet and air is humid. (c) Soil is dry and air is humid. (d) Both soil and air are dry. *(JK CMEE 2000)*

(3) Rate of transpiration is measured by (a) Ganong's potometer (b) Porometer (c) Auxanometer (d) Respirometer. *(AIIMS 2000)*

(4) A sudden increase in CO_2 concentration around a leaf will cause (a) Wider opening of stomata (b) Increase in transpiration (c) Closure of stomata (d) Decrease in transpiration due to closure of stomata. *(AFMC 2001)*

(5) Root hair absorbs water from soil through (a) Turgor pressure (b) Ion exchange (c) Osmosis (d) DPD. *(BHU 1996, 1999, 2000, RPMT 2000)*

(6) Cohesion-tension theory is related to (a) Respiration (b) Ascent of sap (c) Transpiration (d) Photosynthesis. *(CPMT 2001)*

(7) A cell immersed in a solution increases in volume. The solution is (a) Hypertonic (b) Isotonic (c) Hypotonic(d) Either (a) or (b). *(PbPMT 2001)*

(8) The correct order for instrument used in measuring (i) Transpiration (ii) Stomatal size (iii) Atmospheric pressure and (iv) Osmosis is. (a) Potometer, Porometer, Manometer and Osmometer (b) Porometer, Manometer, Potometer and Osmometer (c) Potometer, Manometer, Porometer and Osmometer (d) Manometer, Potometer, Porometer and Osmometer. *(Har. PMT 2002, 2005)*

(9) Main function of lenticel is (a) Transpiration (b) Gaseous exchange (c) Guttation (d) Bleeding. *(CBSE 2002)*

(10) The ingredient used for preserving food stuffs is (a) Vinegar (b) Salt and sugar (c) Sugar and vinegar (d) All the above. *(MPPMT 2002)*

(11) Reduction of water potential due to presence of solute is (a) Solute potential (b) Matric potential (c) Pressure potential (d) Both (b) and (c). *(AMU 2002)*

(12) Root hairs absorb water from soil with the help of (a) Root pressure (b) Suction pressure (c) Turgor pressure (d) Osmotic pressure. *(CPMT 2002)*

(13) Root pressure is maximum when (a) Absorption is high but transpiration is low (b) Absorption is low but transpiration is high (c) Both absorption and transpiration are high (d) Both absorption and transpiration are low. *(JIPMER 2002)*

(14) Solution concentration is higher in the external solution. The solution is (a) Hypotonic (b) Isotonic (c) Hypertonic (d) None of the above.

(15) In CAM plants, stomata are (a) Never open (b) Always open (c) Open during day and close at night (d) Open during night and close during the day. *(AFMC 2003)*

(16) Wilting occurs when there is (a) Transpiration higher than absorption (b) Absorption higher than transpiration (c) High relative humidity of atmosphere (d) Excessive root pressure. *(CBSE 2003)*

(17) Which one is responsible for opening and closing of stomata (a) Rise in *p*H of guard cells, hydrolysis of starch (b) Cytokinins and CAMP required (c) Abscisic acid promotes closure (d) All the above. *(AFMC 2004)*

(18) A plant cell becomes turgid due to (a) Plasmolysis (b) Exosmosis (c) Endosmosis (d) Electrolysis. *(JKCMEE 2004)*

(19) A cell dipped in 0.5 M sucrose has no effect. If it is dipped in 0.5 M NaCl, the cell will (a) become turgid (b) increase in size (c) decrease in size (d) get plasmolysed. *(Kerala 2004)*

(20) Potometer works on the principle (a) root pressure (b) osmotic pressure (c) amount of water absorbed is equal to water transpired (d) potential difference between tip of tube and that of plant. *(AFMC 2005)*

(21) Passive water absorption by root system is due to (a) force created in roots (b) osmotic force in shoot (c) high respiratory activity of root (d) tension in sap due to transpiration. *(CBSE 2005)*

(22) Oozing of water drops from injured leaf edges is (a) bleeding (b) guttation (c) transpiration (d) oozation. *(KCET 2006)*

(23) Accumulation of K^+ ions in guard cells shall cause (a) loss of turgidity (b) decrease in water potential (c) increase in water potential (d) exosmosis. *(Orissa 2006)*

(24) **A and B** are contiguous cells. **A** has OP = 10 atm, TP = 7 atm and DPD = 3atm. **B** has OP = 8 atm, TP = 3 atm, DPD = 5 atm. The result would be (a) no movement of water (b) equilibrium between the two (c) movement of water from **A** to **B** (d) movement of water from **B** to **A**. *(Gujarat 2007)*

(25) Opening of stomata is not affected by (a) N_2 (b) K^+ ions (c) Starch (d) None of the above. *(CBSE 2007)*

(26) Rupture and fractionation of water column present in tracheary elements does not occur during ascent of sap due to (a) transpiration pull (b) weak gravitational pull (c) cohesion and adhesion (d) lignified thick walls. *(DPMT 2008)*

(27) Water potential of pure water and its solution are (a) 0 and 1 (b) 0 and 0 (c) 0 and more than one (d) 0 and less than 1. *(CBSE 2008)*

(28) In walls of guard cells, cellulose microfibrils are arranged (a) obliquely (b) radially (c) transversely (d) taugentially. *(Manipur 2009)*

(29) Solute potential of a solution is always (a) = 0 (b) < 0 (c) > 0 (d) between 0.1 to 1.0. *(AMU 2009)*

(30) Loss of water from tip of leaves is called (a) Guttation (b) Transpiration (c) Evaporation (d) Respiration. *(DPMT 2010)*

(31) Difference between osmotic pressure is (a) DPD (b) Osmotic potential (c) Solute potential (d) Transpiration pull. *(MP PMT 2010)*

(32) Accumulation of which one of the following acids results in closure of stomata (a) Malic acid (b) Aspartic acid (c) PEP (d) OAA. *(Wardha 2011)*

Assertion and Reason Type Questions

1. **Assertion**. Cut stumps pull the water column upwardly.
   Reason. Transpiring leaves show exudation of sap.
   (A) (B) (C) (D) *(AMU 2011)*

2. **Assertion.** Stomata remain open during the day time.
   Reason. Stomata help in exchange of gases.
   (A) (B) (C) (D) *(AIIMS 2001)*

ANSWERS

17. (a) — zero (b) — lower (c) (i) — Transpiration (ii) — guttation (d) Antitranspirants.

Multiple Choice Questions (With Answers)

(1) —d (2) —a (3) —a (4) —d (5) —c (6) —b (7) —c (8) —a (9) —b (10) —d
(11) —a (12) —b (13) —a (14) —c (15) —d (16) —a (17) —d (18) —c (19) —d (20) —c
(21) — d (22) —a (23) — b (24) —c (25) —a (26) —c (27) —d (28) —b (29) —b (30) —a
(31) —a (32) —a

Assertion and Reason Type Questions

(1) —B (2) —B